

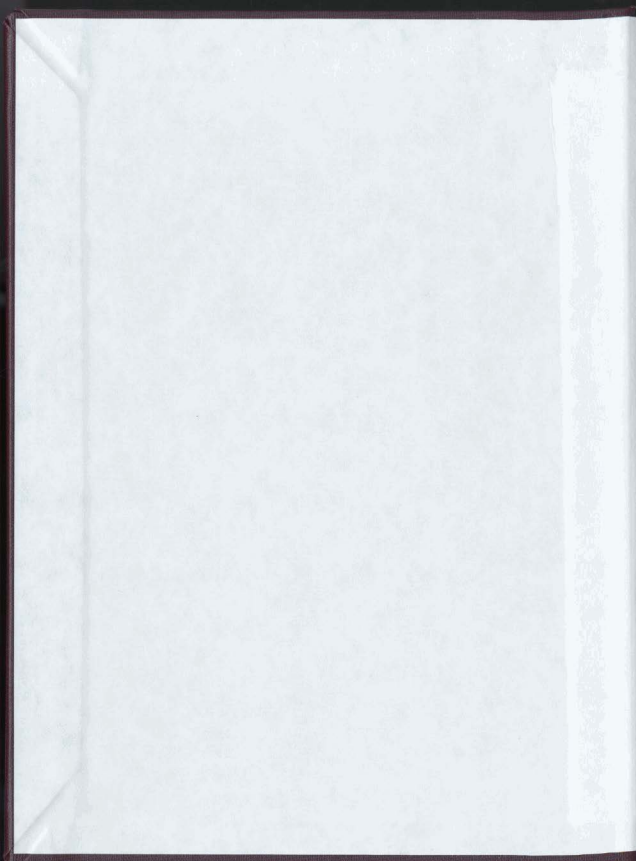
SPATIAL DISTRIBUTION OF FEMALE TABANIDAE
AND SIMULIIDAE (DIPTERA) AMONG DIFFERENT
TERRESTRIAL HABITATS IN CENTRAL NEWFOUNDLAND

CENTRE FOR NEWFOUNDLAND STUDIES

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JERI L. GRAHAM



SPATIAL DISTRIBUTION OF FEMALE TABANIDAE AND SIMULIIDAE
(DIPTERA) AMONG DIFFERENT TERRESTRIAL HABITATS
IN CENTRAL NEWFOUNDLAND

by

© Jeri L. Graham

A thesis submitted to the School of Graduate Studies
in partial fulfilment of the requirements for the degree of
Master of Science

Department of Biology
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ABSTRACT

The spatial distribution of female Tabanidae and Simuliidae among terrestrial habitats was investigated during June-July of 1988 and 1989 in central Newfoundland. Tabanid collections from modified Manitoba and Box traps consisted predominantly of Chrysops species (>93%) with a much lower proportion of Hybomitra species. The four most common species in both years were C. excitans, C. frigidus, C. furcatus and C. zinzalus. In blackfly collections, sampled using dry-ice-baited sticky traps or a combination of landing counts and sweep netting, there was a predominance (>95%) of Eusimulium euryadminiculum, an ornithophilic species; Simulium venustum/verecundum complex and Prosimulium mixtum were also present.

Tabanids were collected from five different habitat types: black spruce forest, fen, bog, regrowth and dirt road. Tabanid abundance was generally lowest on the bog and road, in 1988, and lowest on the regrowth and road in 1989. In both years, tabanids were most abundant in the fen. Factors affecting spatial distribution, including distance from larval habitat, dispersal ability of adults and presence of nectar sources or hosts in a habitat are discussed, as well as the

effect of trapping methods on relative abundance and species composition.

Of the four most common tabanid species, C. excitans and C. furcatus appeared to locate the traps more efficiently in open habitats while C. frigidus and C. zinzelus were trapped most often in a wooded habitat. Clearing of forested land during clear-cut logging operations will likely cause a shift in species composition from the preferentially sylvan species to those preferring open habitats.

Blackflies were collected from three different habitats: fen, woods and regrowth area. These collections support the idea of habitat preferences for some species of biting flies, since blackflies, almost exclusively Eusimulium euradminiculum, were trapped primarily in the fen and rarely in the woods.

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INTRODUCTION

The adult females of many deer fly, horse fly (Diptera (Brachycera): Tabanidae) and blackfly species (Diptera (Nematocera): Simuliidae) are known to blood feed (Wenk 1981, Teskey 1990) and, in doing so, harass the host upon which they are feeding (Fredeen 1969, Lewis and Leprince 1981, NRCC 1982, Teskey 1990). Tabanids blood-feed primarily on large, warm-blooded animals (Teskey 1990) although they likely make some use of small mammals, birds and reptiles (Smith et al. 1970, Chvála et al. 1972, Lewis and Bennett 1977). Blackflies may be classified as either mammalophilic or ornithophilic (Wenk 1981) depending on their host. In Canada, deer flies and horse flies are widely distributed south of the tree line, especially in areas where moist soil, marshes or bogs provide breeding habitats (Pechuman and Teskey 1981). Blackflies are common in areas where streams or rivers provide suitable habitat for larval development (Peterson 1981).

The present research was carried out in conjunction with a study, by the Newfoundland and Labrador Wildlife Division, to determine the effects of logging on woodland caribou (Rangifer tarandus L.) in the Northwest Gander-Great Gull-Southwest Gander River region of central Newfoundland.

Studies of woodland caribou on the Avalon Peninsula, Newfoundland, suggested that the seasonal dispersal of those caribou from open barrens into forest cover around the beginning of July was a means of seeking relief from biting insects (Bergerud 1974). Of concern, then, in the NW Gander area, was the destruction of potential "insect-relief" habitat by clear-cut logging operations. Comparing the distribution of simuliids and tabanids, in open habitats and forested areas, was the first step in testing the hypothesis that fly attack rate differs between habitats and thus influences caribou habitat preference.

The behavioural response of caribou and other ungulates to attack by simuliids or tabanids is indicative of the severity of harassment. An ungulate being harassed by biting tabanids will exhibit head and body shaking, biting at the fly, scratching with a hoof and sudden bursts of running (cattle: Lewis and Leprince 1981, Perich et al. 1986; caribou: Helle and Aspi 1984) all aimed at removing the flies or preventing them from settling. Cattle will stop grazing and sometimes stampede when blackflies become very abundant (Golini et al. 1976, Fredeen 1977).

Harassment by biting flies has a potentially negative effect on the health of the animals being harassed. Changes in activity pattern have been well-documented for caribou, which tend to increase the amount of time spent walking,

standing, trotting and running while decreasing the time spent feeding and lying down (White et al. 1975, Reimers 1980, Downes et al. 1986). Such a shift in activity can lead to reduced rates of growth and fattening during the summer (Reimers, 1980). This can, in turn, affect the growth, and ultimately, the survival of calves from females which have a low nutritional status (Helle and Tarvainen, 1984).

In many cases, animals select habitats which reduce the rate of attack by biting flies. Cattle may move into pools of water, dense brush or inside buildings to escape attack by blackflies (Fredeen 1969) and horses have been observed to move to bare sandy areas which have a decreased level of tabanid harassment (Duncan and Cowtan 1980, Hughes et al. 1981). Barrenground caribou will move to putative insect-relief space at increased altitudes in mountains, and on wind-swept ridges, snow patches and unvegetated areas (Skoog 1968, White et al. 1975, Downes et al. 1986). Woodland caribou have been reported, on the one hand, to use shorelines, exposed ridges or open muskeg for relief from biting insects (Edmonds and Bloomfield 1984) but, as mentioned earlier, a move from open barrens to forested areas has also been suggested as a response to insect harassment (Bergerud 1974).

Harassment results from the blood-feeding activities of the females of many species of tabanids and simuliids which need the additional protein of a blood meal to complete their

cycle of ovarian development. Of the four genera of Tabanidae present in Newfoundland, all species of *Chrysops*, *Hybomitra* and *Tabanus* are known to blood-feed on mammals but, in the genus *Atylotus*, *A. thoracicus* (Hine) has never been observed taking a blood-meal (Teskey 1990). Many tabanid species can complete one gonotrophic cycle autogenously before mating and seeking a blood meal (Anderson 1971, Leprince and Lewis 1983) although a complete list of species which have this capability has not yet been compiled (Teskey 1990). Of the 21 species of blackflies described for the island, only a few are considered major pests of mammals: the *Simulium venustum/verecundum* complex, *Prosimulium mixtum* Syme and Davies, *Stegopterna mutata* (Malloch), *Simulium vittatum* Zetterstedt and *Simulium decorum* Walker (Lewis and Bennett 1973, McCreadie 1983). Furthermore, many blackfly species do not need a blood meal to produce the first batch of eggs, including *P. mixtum*, *St. mutata*, *S. vittatum* and *S. decorum* (Lewis and Bennett 1973).

If host animals, such as caribou, appear to choose certain habitats in order to reduce the amount of insect harassment, the question arises as to why we might expect differences in harassment potential between habitats. The extent to which the preferred habitats of the host and the adult fly overlap will be a key factor influencing the amount of harassment (Smith *et al.* 1970). A number of studies indicate that tabanids and blackflies do not randomly disperse

but rather show differences in abundance and species composition between habitats (simuliids: Bennett and Fallis 1971, Baldwin et al. 1975, Martin 1987; tabanids: Smith et al. 1970, Dale and Axtell 1976, Thibault and Harper 1983).

The final habitat of the adult female depends partly on its ability to disperse from the habitat in which the larvae develop, as well as the requirements of the adult fly. Tabanid larvae are generally found in wet or moist conditions in ponds, streams, damp soil or sphagnum bogs although a few are reported to develop in relatively dry soil or rotting wood (Pechuman 1981). The development of blackfly larvae and pupae is usually restricted to running water (Peterson 1981). Movement away from the emergence site brings the adult fly into a habitat where it is likely to contact a host. Release and recapture experiments with tabanids have recorded flights up to 6.8 km (Sheppard and Wilson 1976). Studies of blackfly dispersal (Baldwin et al. 1975, Fredeen 1977, Ryan and Hilchie 1982) indicate that blackflies generally travel farther from the emergence site than tabanids (Bennett and Smith 1968, Sheppard and Wilson 1976). Wenk (1981) classified blackfly movement to a new habitat as either "dispersal", movement determined by the flight capabilities of the insect, or "migration" in which the insect has less control and is carried great distances by the wind. After emergence, the females of both tabanids and simuliids may engage in mating

and nectar feeding before seeking a blood meal (Sutcliffe 1986, Teskey 1990).

Habitat selection was defined by Smith (1966) as the first step in host-seeking, before specific orientation behaviours are brought into play. Once located in a 'preferred' habitat, vision and olfaction are used in an interactive manner by tabanids and simuliids orienting to a host (Bradbury and Bennett 1974b, McElligott and McIver 1987). It would seem that tabanids rely on visual features as the initial mechanism for orienting to the host since olfaction most effectively enhances the attraction at distances of 3 m or less (McElligott and McIver 1987). For blackflies, odour is thought to be a long- to middle-range attractant, involving specific host odours and carbon dioxide, with vision directing orientation at closer ranges, between 0-180 cm (Bradbury and Bennett 1974b). Several factors such as colour, contrast with the environment and shape of the target are involved in the visual attraction of tabanids (Allan and Stoffolano 1986) and simuliids (Bradbury and Bennett 1974a, 1974b). The relative importance of sight, carbon dioxide emission and host odour may vary with habitat for host-seeking blackflies (Thompson 1976a, 1976b) and possibly for tabanids, although this has not been studied. An understanding of visual and olfactory attraction has been used to develop methods of trapping and sampling biting flies.

The present study investigated the distribution of host-seeking tabanids and simuliids between a number of vegetatively different habitats in caribou summer range. The initial objective was to test whether forested areas had a sufficiently lower biting fly population to support the suggestion that forest habitats provide a "fly-relief" habitat. The study assessed the relative abundance and species composition between forested and open areas, including areas disturbed by clear-cut logging and road building activities.

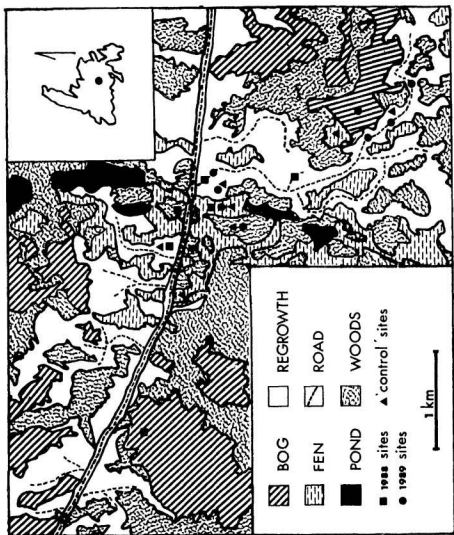
METHODS

A. STUDY AREA

The study area was located in the NW Gander-Great Gull-SW Gander River drainage basin of central Newfoundland (Fig. 1) (55° 15'W, 48° 30'N). This region of the province is located in the Central Uplands climatic zone (Banfield 1983) and was designated as the Central Newfoundland Forest ecoregion by Damman (1983). A pulp and paper company has based cutting operations in this area since 1981 which has resulted in a network of dirt roads providing access to the area.

Trapping programs to compare tabanid and blackfly populations in different habitats were located in a 12 km² region around Owl Pond (Fig. 1). This area was chosen as the study site because it has a wide variety of habitats representative of the types of habitats found throughout the area of cutting operations. The sampling was limited to this relatively small area to avoid the possible effects of large-scale, regional distribution patterns of tabanids and blackflies (Teskey 1960, Matthyse et al. 1974, Golini and Wright 1978). All sites were easily accessible from the logging roads. Three main rivers, NW Gander, Gull and SW Gander, are within 4-12 kilometres of the study area; several

Figure 1. "NW Gander" study area located around Owl Pond in the NW Gander-Great Gull-SW Gander River basin, NF. Sites are identified where trapping was carried out to compare abundance of tabanids in different habitats in 1988 (■) and 1989 (●) and where abundance in the same type of habitat was compared in 1989 (▲). (One of the wooded areas used in "control" trapping was located to the west of the main study area and is not shown on this map). Trapping to compare abundance of blackflies in different habitats was located in the fen, woods and regrowth areas used for tabanid trapping in 1989.



small ponds (1 km² or larger) are near or within the area.

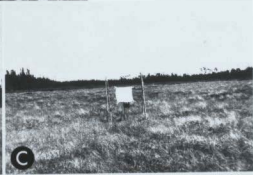
B. HABITAT TYPES

Five major habitat types (Fig. 2) were selected for comparison in both the 1988 and 1989 field seasons: black spruce forest, fen, bog, regrowth and dirt road. Peatlands were placed into a general category as described by Wells and Pollett (1983) while forest classification was outlined by Meades and Moores (1989). Plants were classified according to Peterson and McKenny (1968) and Ryan (1978). The following habitat descriptions also include a general description of exposure to wind and soil moisture. Since a number of different sites within each type of habitat were sampled, and because some of the sites differed between field seasons, the descriptions refer to the habitat type in general, as opposed to a specific location.

1. Forest

The forest was a combination of Black Spruce-Feathermoss/very dry and Cladonia-Kalmia-Black Spruce forest types (Fig. 2A). It was comprised almost entirely of black spruce (Picea mariana (Mill.) B.S.P.), about 10-12 m high, with an open, mossy understorey. Sheep laurel (Kalmia

Figure 2. Five habitat types used in comparisons of tabanid and simuliid abundance: A) Forest B) Fen C) Bog D) Regrowth E) Road.



angustifolia L.), Labrador tea (Ledum groenlandicum Oeder), bunchberry (Cornus canadensis L.) and caribou moss (Cladonia spp.) were abundant in clearings. The ground was damp and mossy in the canopied areas but drier in the clearings. The forest was the most sheltered of all the habitats with little wind detected there even on the windiest days.

2. Fen

Fens (Fig. 2B) were typified by grasses and sedges, between 20-50 cm high although sphagnum moss (Sphagnum spp.) was common throughout the area. Occasional stunted larch trees (Larix laricina (DuRoi) K.Koch) were present. Conditions were wetter than in any other habitat; large pools of water (up to 100 m²) were common and, in one fen, a stream was present. This habitat was open; usually bordered on one side by a road and surrounded on the remaining sides by black spruce forest at least 25 m away.

3. Bog

The large, domed bogs (Fig. 2C) had sphagnum moss as the dominant vegetation, as opposed to the predominantly grassy nature of the fens. The vegetation was generally low (under 50 cm) and included caribou moss, bakeapple (Rubus chamaemorus L.), leatherleaf (Chamaedaphne calyculata (L.) Moench),

crowberry (*Empetrum nigrum* L.), sheep laurel and Labrador tea. Raised clumps of stunted black spruce, "tuckamore", were scattered throughout the area. Conditions were generally damp but not as wet as in the fen; open pools (up to 100 m²) were present only on the edges of the bog. The two bogs used in the study, both bordered by black spruce forest, were larger and more exposed than the fens.

4. Regrowth

A number of open and exposed regrowth areas (Fig. 2D) had resulted from cutting operations which were carried out in the Owl Pond region about two to three years before this study began. Patches of bare ground were present although some regeneration by low herbaceous plants and scattered small shrubs had taken place. The dominant shrubs were sheep laurel and small black spruce while various mosses, blueberry (*Vaccinium angustifolium* Ait.) and bunchberry were common groundcover. Regrowth areas were generally bordered by a logging road on one or two sides and black spruce forest on the remaining edges. The soil was often rocky with little humus and usually dry.

5. Road

The road habitats were bulldozed feeder roads (Fig. 2E),

about 10 m wide, with no vegetation and normally bordered by clear-cut areas. They were exposed to the wind except where large, earth banks, up to 2 m in height, had been piled up during construction.

C. TRAP DESIGN

A number of trapping methods were used to assess the relative abundance and species distribution of tabanids and simuliids between different habitats. All sampling methods were designed to collect only adult females which were searching for a blood meal. It was assumed that the ability of a female tabanid or simuliid to locate a trap, composed of visual and olfactory stimuli, in a certain habitat is comparable to its ability to locate a host, such as a caribou, in that habitat. This assumption is based on a considerable body of data concerning the host-seeking behaviour of tabanids and simuliids (Smith 1966, Browne and Bennett 1980, Sutcliffe 1986, McElligott and McIver 1967).

1. Traps for sampling Tabanidae

Two types of carbon-dioxide-baited traps were used to collect tabanids; a Manitoba trap (Fig. 3A) modified from Thorsteinson et al. (1965), and a Box trap (Fig. 3B) modified from Bennett and Smith (1968). Manitoba traps were used in the 1988 season since a number of studies found this trap to

Figure 3. Two types of traps for sampling Tabanidae:
A) Manitoba trap B) Box trap.



be efficient in trapping horse flies (Bennett and Smith 1968, Pechuman and Burton 1969, Thompson 1970). The primary collection method was changed to Box traps, however, in 1989 since preliminary studies in 1987 using these traps (Graham, unpub.) had collected higher numbers of tabanids than did the Manitoba traps in 1988 (see also section 3.A.5).

Both the Manitoba and Box traps used a combination of visual and olfactory features to attract tabanids. A dark blue target was used in both cases, a circle painted on a baffle for the Manitoba trap and a blue bucket for the Box trap. Browne and Bennett (1980) found dark blue to be consistently attractive to Chrysops and Hybomitra. Traps were baited with carbon dioxide, in the form of dry ice (releasing appx. 250 mL CO₂/min), since its presence greatly increases trap catches of tabanids (Roberts 1971, Knox and Hays 1972).

i) Manitoba trap

The canopy of the Manitoba trap, constructed from white netting, formed a cone that was attached at the top to a ring of PVC pipe (ca. 12 cm diameter x 4 cm length) fitted inside a larger cylinder of PVC pipe (ca. 15 cm diameter x 20 cm length) and secured by two screws. A collecting jar, fitted with a one-way conical entrance, was placed into the top of the larger PVC pipe. The trap was supported by a central pole (1.5-1.75 m high), attached with a cross-screw arrangement

to the centre of the pipe, and four guy ropes were used to stake out the sides of the canopy. A dark blue (Chevron Blue, Canadian Tire Corp., Toronto, Ontario, Canada) circle about 50 cm in diameter was painted on each side of an X-shaped baffle hung under the canopy. The baffle was added to the trap in an attempt to increase the efficiency of the trap for flies parasitic on caribou, namely warble flies (Oedemagena tarandi (L.)) and nose bots (Cephenemyia trompe (Modeer)) (J. Anderson pers. comm.), which, since they are known to harass caribou, were also of interest. The target, on the baffle, was hung between 0.5 and 1 m high which is similar to the optimum height discovered by Joyce and Hansens (1968), Schulze et al. (1975) and Roberts (1976). Traps were baited with dry ice (ca. 250 g) placed inside a dark blue bucket which was hung at a height of 1 m from the central pole. The dry ice was insulated with layers of sphagnum moss to extend the time of emission, and carbon dioxide was released through five holes (9 mm diameter) in the bottom of the bucket. The collecting jar with insects was either placed in a freezer or a small square of Vapona® (dichlorvos insecticide) was placed in the opening.

The target was changed in 1989 for two reasons: there were very few parasitic flies trapped using the target on the baffle, and the use of a baffle considerably increased the

time needed to set up a trap. Thus, in 1989, three dark blue buckets tied together side by side were used as a target and no baffle was used. These buckets were hung from the central pole, at a height of about 1 m, and baited with carbon dioxide in the manner described previously.

ii) Box trap

The Box trap was a simple box (ca. 50 x 50 x 50 cm) constructed from white netting and open on the bottom except for a 10 cm internal flap which decreased the loss of flies crawling down the sides and out the bottom. The net was supported by strings at each corner, top and bottom, which were tied to four poles (or trees). The bottom of the box was approximately 1 m above the ground and the target, again a dark blue bucket, was hung so that the top was just below the bottom of the box. The bucket was baited with dry ice in the same manner as for the Manitoba traps. In order to collect the flies inside, the bottom ties were undone, a drawstring along the bottom edge of the net was closed and the trap untied from the poles. The net was placed in a freezer after which flies were picked or shaken out of the net.

Tabanids were identified using keys by Teskey (1990) and McCreadie (unpub.), a key to species of tabanids in Newfoundland and Labrador based on those by Stone (1938), Pechuman et al. (1961), Philip et al. (1973), Lewis and

Bennett (1977) and Teskey (1984). Sample specimens of each species collected were sent to the Biosystematic Research Institute in Ottawa for confirmation of identification.

2. Traps for sampling Simuliidae

Two methods of sampling blackflies were used, a carbon-dioxide-baited sticky trap, as described by Martin (1987), and a sampling procedure combining landing counts and sweep netting. Sticky traps catch large numbers of blackflies and can be used to sample over an extended time period whereas landing counts and sweep netting enable a number of samples to be collected in a relatively short time.

i) Sticky trap

Carbon-dioxide-baited sticky traps were identical to those constructed by Martin (1987). Plastic buckets (6 l capacity, 21 cm diameter, 19 cm high) were painted dark blue. The sides of the bucket were covered with a sheet of thin plastic (Glad Cling Wrap[®], Union Carbide Canada Ltd., Toronto, Ont., Canada) and sprayed evenly with Tanglefoot[®] (Tanglefoot Co., Grand Rapids, Mich., U.S.A.), a sticky substance which trapped blackflies landing on the bucket. Traps were baited with dry ice (ca. 250 g) as described previously (section C.1.i.). The buckets were tied to a branch on a pole at a

height of about 1 m from the ground. The plastic containing the blackflies was soaked in kerosene to loosen the specimens. Blackflies were identified according to keys by Davies et al. (1962) and Peterson (1970); Drs. M.H. Colbo and P. Adler assisted with the identification.

ii) Landing counts/sweep net

Landing counts were carried out by an observer who would count the number of blackflies which landed on a dark-coloured board (20 x 30 cm) during a one minute period. Two people, each with an identical board, stood in the same habitat facing the same direction and at least 10 m apart. After an initial 3-5 minute period, which allowed the blackflies in the area to detect and locate the people, the observers then stood holding the board in front of them and, simultaneously, made three counts each of one minute. After the counts, a sweep net was used to collect blackflies flies for later identification. The bottom of the net, containing the flies, was placed into a killing jar holding a piece of dichlorovos insecticide. The blackflies were later preserved in 70% ethanol.

D. SAMPLING METHODS

1. Tabanidae

i) Comparison of abundance between habitats

Relative abundance and species distribution of tabanids

in different habitats was assessed by placing several traps in each of the different habitats and operating them simultaneously. (See Appendix A for dates of tabanid sampling.) In 1988, five habitats were sampled at the same time: woods, fen, bog, regrowth and road. Since the number of traps and amount of dry ice was limited, the sampling in 1989 was broken into two groups to increase the number of traps in each habitat. The first comparison included woods, fen and regrowth; the second compared the woods with bog and road habitats. Each sample group in 1989 contained a wooded area, a natural open area, and an open area created through logging activities.

In each of the habitats, traps were placed in locations which typified the characteristics of that habitat. The traps were located at least 10-15 m apart to decrease the amount of interference with other traps. Since carbon dioxide is most effective over a range of 3 m (McElligott and McIver 1987), it was assumed that the carbon dioxide plumes from one trap would affect catches at the other traps only minimally. There was a distance of 25 m or more from each trap to the boundary of a different habitat. At that distance, a trap in the woods could not be seen from an adjoining road, regrowth or peatland. For traps in the woods, target visibility was estimated based on percent of the target which was visible. The average was taken of four estimates, one from each side of

the trap, as viewed by an observer three metres away from the trap at an eyelevel of one metre.

Traps were baited with dry ice early in the afternoon (between 1330-1430 h Newfoundland Daylight Savings Time) on sunny days with temperatures above 20 °C, conditions considered favourable for high tabanid activity (sunshine: Joyce and Hansens 1968, Burnett and Hays 1974, temperature: Tashiro and Schwardt 1949, Miller 1951). Since the dry ice would only last 5 to 6 hours, trapping was carried out under conditions of expected high activity to ensure the largest possible sample sizes for comparing the different habitats. Since there is some variability in tabanid activity during the day (Roberts 1974, Thorpe and Hansens 1978, Hollander and Wright 1980), the order of baiting the traps was reversed on some days to decrease any differences caused by factors associated with time of day. Comparisons were run over a number of days (4 to 6) to minimize the effects of variable meteorological conditions.

In 1988, two Manitoba traps were placed in each of the five habitats. On days when traps were baited, the collecting jars were changed at one and a half or two hour intervals to increase the sample size. (For example, two collections from each of the two traps were considered to be four samples.) The final collection was made before sunset to ensure that any flies on the inside of the tent that did not make it to the

collecting jar would not have dropped to the ground and out of the trap. The 1989 trapping procedure involved setting up four Box traps in three habitats at a time. The traps were emptied only once a day, thus eliminating any time effects caused by collecting every two hours.

ii) Comparison of abundance within a habitat type

To ensure that the sites chosen for comparisons of tabanid abundance between different habitats were representative of the general habitat type, a control was carried out, in 1989, to compare sites within a habitat type. The wooded area used in comparisons between habitat types (section 2.D.1.i.) was compared to two other wooded areas in the Owl Pond region. The fen and regrowth used in comparison trapping between habitats were similarly compared to two other fens and regrowth areas respectively. The sites chosen, although in the same habitat classification, had some visible differences. The fen used in the fen/woods/regrowth comparison had a small stream running through it. A stream was not present in either of the other two fens used in the control comparison and those fens generally had a greater area covered by standing pools than the fen with the stream. The two woods sites chosen as sites in the control comparison were a mixture of Black Spruce-Feathermoss/very dry and Cladonia-Kalmia-Black Spruce forest types, as was the forest site used

days between June 16-25, 1989 near a base camp located about 11 km from the Owl Pond site. This trapping was used to monitor tabanid activity early in the season to determine when numbers were high enough to begin comparison trapping between habitats. In 1989, trapping was discontinued in early August after trap catches had sharply declined.

2. Simuliidae

1) Comparison of abundance between habitats

Four sticky bucket traps were placed in each of three habitats; woods, fen and regrowth, to compare the abundance of blackflies between habitats. (See Appendix B for dates of blackfly sampling.) On five days in June, 1989, the traps were baited at 1400 h (Newfoundland Daylight Savings Time) with enough dry ice to last for five to six hours. Dry ice was distributed as quickly as possible to the trap sites to reduce the number of flies attracted to the person baiting the traps and to ensure the traps were all operating at approximately the same time. The buckets were picked up in the late evening or early morning when temperatures were cool enough to prevent activity of blackflies, again reducing the number of flies on the traps which had been attracted to the collector. The number of blackflies on each bucket was counted before the plastic was removed and the trap rewrapped, resprayed and set out in the morning.

in comparisons between different habitat types. The three regrowth areas selected for comparison had been cleared during the same cutting year.

Manitoba traps were used since the Box traps were being used in the comparisons between different habitats. Three traps were set up at least 15 m apart at each of the three sites and baited in the same manner as previously described. The traps were run for three days for each of the three control comparisons. The collecting jars, on the Manitoba traps, were left on for the entire afternoon, making up a single trapping period.

In 1988, a comparison was carried out between three different woods sites; a mature black spruce forest, a drier and more open black spruce forest, and locations in a mature forest which had previously been used as bedding sites by caribou. Manitoba traps with baffles were used in the comparison; they were set up and baited as described for other comparisons.

iii) Seasonal occurrence

Although sampling to determine the full period of tabanid seasonal activity was not carried out, tabanids were captured by chance with a sweep net or in a vehicle both earlier and later in the season than the above-mentioned sampling programs. In addition, two box traps were operated on sunny

Blackfly abundance was also compared, on June 15 and 16, using a combination of landing counts and sweep netting. Two people sampled three habitats in turn: a wooded area, a fen and a large clearing in the woods (ca. 20 x 40 m). A sampling period was defined as a set of counts and sweeps in each of the 3 habitats. Starting in the first habitat, the two collectors would record initial data, carry out three landing counts on the board, collect a sweep net sample and then move onto the next two habitats in turn. The location was chosen so that the three habitats were in close proximity to each other (within 100 m) and very little time elapsed while the collectors walked from one to another. After the sampling procedure had been carried out in each of the three habitats, the collectors would begin again (sampling period #2) in the first habitat.

To investigate the effect of different times of day on spatial distribution, a fen and wooded area were sampled at two different times on June 20, 1989. The same collection procedure, involving counts and sweeps, was carried out for two sampling periods in the morning and two in the afternoon.

3. Meteorological conditions

Standard meteorological measurements were taken three times daily; morning, noon and evening, at the base camp. These measurements included temperature, wind speed (measured

with a hand held anemometer), wind direction, relative humidity (measured with a sling psychrometer) and a description of cloud cover.

E. ANALYSIS OF DATA

1. Tabanidae

A non-parametric method of analysis was chosen since the trap data did not meet the requirements for parametric statistics. With tabanid data, total abundance (based on a standardized two hour catch) was compared between habitats using a Kruskal-Wallis test, which involves a system of ranks, and a Tukey-type analysis for multiple comparisons (Zar 1974). This type of analysis was used for the seasonal total of tabanids as well as for the totals of the two genera, Chrysops and Hybomitra, separately. The differences between habitats was considered for all trapping days combined and for each individual sampling day. Abundance of the most common species of tabanids, those making up greater than 5% of the total catch, was compared between habitats using a Kruskal-Wallis and Tukey-type analysis for a combination of all the trap days in a given comparison and for separate daily totals. Days were excluded from the analysis if the maximum number of a species was below 10 in the habitat with the highest catch of that species for the day.

From the 'control' trapping between three different

wooded areas, fens and regrowth areas, trap totals were again analyzed with a Kruskal-Wallis procedure. The same procedure was used to see if significant differences were present between the four traps within each of the habitats used in the fen/woods/regrowth and bog/woods/road comparisons.

Trap catches of tabanids were combined for each trapping day (from trapping comparing different habitat types) and a non-parametric Pearson correlation analysis (Zar 1974) was run comparing daily catches to wind and maximum temperature, as measured at a base station. In the case of traps in the woods, a correlation analysis was carried out relating total catch in each trap to a visibility factor for each trap based on the percent of target visible.

2. Simuliidae

A Kruskal-Wallis analysis, using average ranks, was used to determine whether there were significant differences in blackfly abundance between the fen, woods and regrowth based on sticky trap counts. A Tukey-type test further elucidated the differences between habitats.

The same analysis was used for landing counts, using each count as a replicate, except when only two habitats were involved in the comparison in which case a non-parametric Mann-Whitney test (Zar 1974) was used.

RESULTS

A. TABANIDAE

1. Overview of trapping results from comparisons between habitats

Overall, 4912 female tabanids were collected during the two seasons of trapping to compare abundance in different habitats (Table 1). Deer flies (Chrysops spp.) made up, by far, the greater proportion of the tabanids sampled: 93.1% in 1988 and 97.0% in 1989. Horse flies (Hybomitra spp.) made up a greater percentage of the catch from the Manitoba traps in 1988 (6.9%) than in the Box traps from 1989 (3.0%).

In terms of individual species, Chrysops excitans Walker was the most commonly collected species in 1988 (65.6 %) while Chrysops furcatus Walker predominated (39.0%) in 1989. In both years, the four most common species of tabanids were C. excitans, C. furcatus, Chrysops frigidus Osten Sacken and Chrysops zinzalus Philip although the relative proportions differed between the two years. Hybomitra lurida (Fallen) and Hybomitra affinis (Kirby) were the most commonly trapped horse flies in 1988. Hybomitra affinis and Hybomitra arpadi (Szilady) were the most common species of Hybomitra caught in 1989 and there were relatively fewer H. lurida as compared to

Table 1. Total numbers and proportion of each tabanid species (Chrysops and Hybomitra) trapped in 1988 and 1989 during trapping to compare tabanid abundance between habitats, North West Gander, NF. Manitoba traps were used in 1988; Box traps in 1989.

Species	1988		1989	
	number	(%)	number	(%)
<u>C. ater</u>	11	< 1	7	< 1
<u>C. excitans</u>	998	65.6	853	25.2
<u>C. frigidus</u>	111	7.3	497	14.7
<u>C. furcatus</u>	173	11.4	1322	39.0
<u>C. mitis</u>	1	< 1	0	0
<u>C. nigripes</u>	1	< 1	1	< 1
<u>C. sordidus</u>	9	< 1	18	< 1
<u>C. zinzalus</u>	112	7.4	588	17.3
Total <u>Chrysops</u>	1416	93.1	3286	97.0
<u>H. affinis</u>	41	2.7	23	1.0
<u>H. arpadi</u>	2	< 1	29	1.0
<u>H. epistates</u>	-	-	9	< 1
<u>H. frontalis</u>	2	< 1	11	< 1
<u>H. lurida</u>	9	< 1	8	< 1
<u>H. miniscula</u>	6	< 1	9	< 1
<u>H. zonalis</u>	46	3.0	15	< 1
Total <u>Hybomitra</u>	106	6.9	104	3.0
Totals	1522	-	3390	-

1988 catches.

Although the determination of seasonality was not an aim of the study, plotting the average two hour catch for each trapping day during the study does provide information on the timing of peak activity. In 1988, trapping took place on six days from July 5-24; the peak of activity, particularly for Chrysops spp., started in the third week in July (Fig. 4A). Hybomitra spp. peaked slightly before deer flies although such low numbers were trapped that this result is of uncertain significance. For the four most common Chrysops, there was slightly higher activity during the last three trapping days (July 16,18,24), of note was the high peak for C. frigidus on July 18 (Fig. 5A). Trapping in 1989 took place on 9 days between June 28-July 24. The highest tabanid activity in 1989 occurred earlier in July than in 1988 and both genera peaked in the second week (Fig. 4B). All four of the most common Chrysops were collected in highest numbers during the second week of July (Fig. 5B).

The seasonal range of each species based on occurrence in any trap, not just those used in comparison trapping between habitats, extended from July 4 to August 3 in 1988 (Table 2) and from June 16 to August 2 in 1989 (Table 3). In 1989, two traps were operated near the camp from June 15 until June 28, when trapping to compare different habitats started, to obtain better data on timing of species appearance. Species

Figure 4. Activity of Tabanidae, Chrysops spp. and Hybomitra spp. in the NW Gander study area as indicated by average two hour trap catches during trapping to compare abundance in different habitats:
A) July, 1988 and B) June-July, 1989.

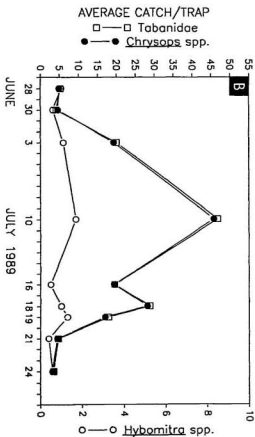
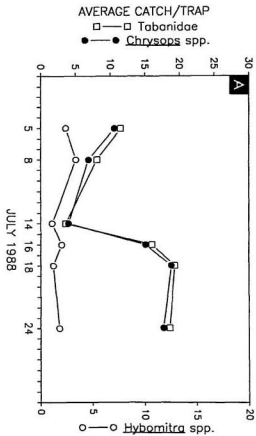
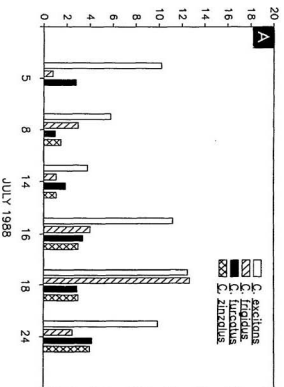


Figure 5. Activity of four common Chrysops spp. in the NW Gander study area as indicated by average two hour trap catches during trapping to compare abundance in different habitats: A) July, 1988 and B) June-July, 1989.

AVERAGE CATCH/TRAP



AVERAGE CATCH/TRAP

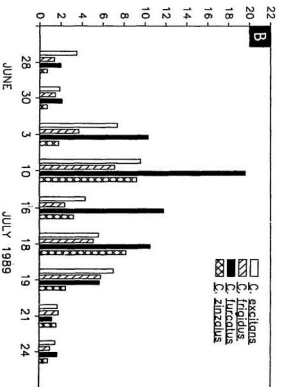


Table 2. Occurrence of tabanid species at the NW Gander study area, NF from July 4 to August 3, 1988. Most sampling was done with Manitoba traps.

	July													Aug.		
	4	5	6	8	10	11	14	16	18	19	21	23	24	29	30	3
<u>H. affinis</u>	+	+	+	+	+	+	+	+	+	+	+					
<u>C. ater</u>	+		+	+	+	+	+	+						+		
<u>C. excitans</u>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<u>C. frigidus</u>		+		+	+	+		+	+	+	+	+	+	+	+	+
<u>C. furcatus</u>		+		+	+	+	+	+	+	+	+	+	+	+	+	+
<u>H. lurida</u>	+	+	+	+	+	+		+		+						
<u>H. zonalis</u>		+		+	+	+	+	+	+	+	+	+		+	+	
<u>C. zinzalus</u>				+	+	+		+	+	+	+	+	+	+	+	+
<u>C. sordidus</u>					+			+	+	+		+				
<u>H. frontalis</u>									+	+	+	+		+	+	+
<u>H. arpadi</u>										+	+					
<u>H. minuscula</u>										+	+	+		+	+	+
<u>C. nigripes</u>										+	+					

Table 3. Occurrence of tabanid species at the NW Gander study area, NF from June 16 to August 2, 1988. Most sampling was done with Box traps.

	June										July										Aug.				
	16	20	21	24	25	28	30	3	4	6	10	11	13	14	16	17	18	19	21	23	24	26	27	1	2
<u>C. ater</u>	+	+	+			+			+		+			+	+			+			+				
<u>H. affinis</u>	+	+	+	+	+	+	+	+	+		+		+		+			+	+						
<u>H. lurida</u>	+		+			+		+			+														
<u>C. frigidus</u>		+				+	+	+	+		+	+	+	+	+			+	+	+			+	+	+
<u>C. excitans</u>			+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<u>H. epistates</u>						+	+	+			+							+							
<u>C. sordidus</u>				+	+	+	+	+	+		+		+		+			+							
<u>H. zonalis</u>			+	+	+	+	+	+			+	+	+	+	+			+	+			+	+	+	
<u>C. furcatus</u>				+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+
<u>C. zinzalus</u>				+	+	+	+	+	+	+	+	+	+	+	+			+	+	+			+	+	
<u>H. arpadi</u>			+			+	+	+	+	+	+	+	+	+				+	+	+					
<u>H. frontalis</u>									+		+		+		+			+	+			+	+	+	+
<u>H. minuscula</u>											+						+	+	+	+		+		+	+
<u>C. nigripes</u>																					+				

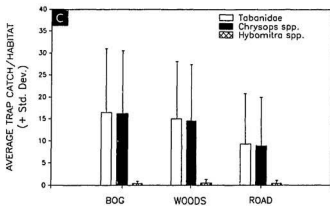
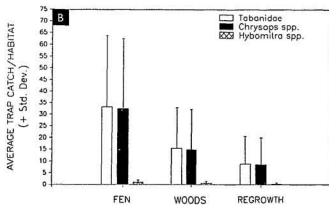
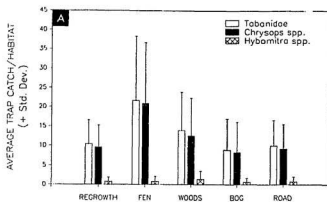
appearing early were Chrysops ater Macquart, H. lurida and H. affinis while the species which appeared later in the season, in both years, were Hybomitra frontalis Walker, Hybomitra minuscula (Hine) and Chrysops nigripes Zetterstedt. Hybomitra lurida had a relatively short season whereas C. excitans, C. frigidus, C. furcatus, and C. zinzalus had relatively long seasons of activity from June throughout July to early August. Trapping in this study did not cover the very beginning or end of seasonal tabanid activity.

2. Comparison of tabanid abundance between different habitats

i) 1988 comparison between regrowth, fen, woods, bog and road

The average two hour catch of tabanids for each of the five habitats during 1988 was 10.4 in the regrowth, 21.6 in the fen, 13.9 in the woods, 8.9 in the bog, and 10.0 in the road (Fig. 6A). A non-parametric Kruskal-Wallis test revealed a significant difference in the total number of tabanids trapped in these five habitats ($p < 0.01$). A Tukey-type comparison indicated that catches in the bog were ranked significantly lower than in the other four habitats. A breakdown into the 2 genera, Chrysops and Hybomitra, revealed a highly significant difference between habitats for deer flies ($p < 0.01$) but no significant difference for horse flies ($p > 0.05$). Catches of Chrysops spp. in the bog ranked

Figure 6. Average two hour trap catch of tabanids in each habitat (+ one standard deviation) in:
A) comparison of abundance between woods, fen, bog, regrowth and road, July 5-24, 1988, B) comparison of abundance between fen, woods and regrowth, June 28-July 16, 1989 and C) comparison of abundance between bog, woods and road, July 18-24, 1989.



significantly lower than in the other four habitats. The average rank was highest in the fen for Chrysops but highest in the woods for Hybomitra.

On a daily basis, two of the six trapping days, July 14 and 16, revealed significant differences between habitats. On those two days, though, the results of the Tukey-type comparison were slightly different; on July 14, the bog was ranked lowest and significantly different from the other four habitats ($p < 0.01$), while on July 16, both the road and the bog were ranked lower than and different from the others ($p < 0.05$). The fen was often ranked highest, except on July 5 and 8 when the woods were highest, but these rankings were not shown to be significant.

ii) 1989 comparison between fen, woods and regrowth

In the 1989 comparison between fen, woods and regrowth, the regrowth ranked lower and significantly different from the woods and fen ($p < 0.01$). The average two hour trap catches for these three habitats were 33.2 for the fen, 15.4 in the woods and 8.9 in the regrowth (Fig. 6B). A significant difference between these habitats was maintained for separate totals of deer flies and horse flies ($p < 0.01$). For both Chrysops spp. and Hybomitra spp., the regrowth was again ranked differently, and lower, than the other two habitats. The fen was always ranked highest although the Tukey-type test did not show it to

be different from the woods.

Considering each of the five trapping days separately, only the two days in June showed significant differences ($p < 0.05$); the regrowth ranked significantly lower than the woods and fen on both days. The three days in July did not show significant differences between the fen, woods and regrowth although the results of the Kruskal-Wallis test were close to the significance level. On all five trapping days, the fen was ranked highest.

iii) 1989 comparison between bog, woods and road

The set of habitat comparisons in 1989, from July 18 - 24, did not show significant differences in tabanid abundance between the bog, woods and road when all four trapping days were considered together, although the results of the Kruskal-Wallis test were of borderline significance. The average trap catches for each habitat were 15.0 for the woods, 16.54 in the bog and 9.3 for the road (Fig. 6C). Differences were detected for totals of Chrysops spp. ($p < 0.05$) but a Tukey-type test was not able to distinguish which of the three habitats differed. Totals of Hybomitra spp. alone showed no significant differences, when analyzed by a Kruskal-Wallis test.

When the four trapping days were considered separately, a difference was detected for only one of the days (July

21) ($p < 0.05$). A Tukey-type test for the July 21 results could not separate which habitats were different, although the road was ranked lowest on each day in this set of comparisons.

iv) Summary of tabanid abundance between different habitats

The overall impression of the five habitats compared in 1988, based on mean ranks of abundance, was that the fen was the most preferred habitat for tabanids, especially Chrysops. The woods had the highest mean rank for Hybomitra spp., a result which is of limited significance since numbers were generally low. There was no consistent ranking of tabanid abundance in the other four habitats (bog, regrowth, road, woods).

In the fen/woods/regrowth comparison of 1989, the fen was consistently ranked high and generally the regrowth was lowest. It could not be ascertained to which habitat the woods were more similar, in terms of tabanid abundance. The bog/woods/road comparison ranked the bog consistently higher than the woods or road, although the average rank for abundance in the wooded area was generally not very different from that of the bog. As mentioned previously, the road was always ranked lowest.

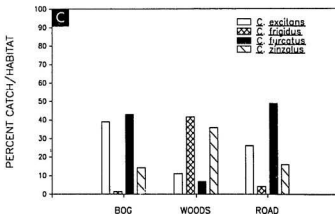
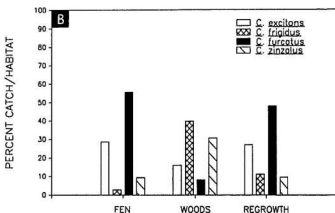
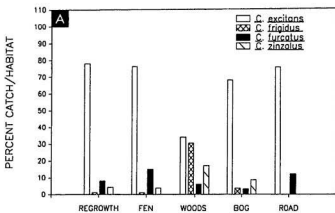
3. Comparison of abundance of tabanid species in different habitats

Most species of tabanids were trapped in numbers too low to allow a meaningful comparison between habitats. Individual species of Hybomitra never made up more than 2% of the total catch in any one habitat and the genus as a whole comprised less than 10% of the catch. Of the Chrysops species, only four species were sufficiently abundant for analysis of catch differences between habitats; none of the remaining species made up more than 2% of the catch in a habitat.

There were some clear differences in species distribution between the four most common Chrysops species: C. excitans, C. frigidus, C. furcatus and C. zinzelus (Fig. 7). Defining the catch of each species as percent of the total tabanid catch in a given habitat gives an idea of the species most likely to be encountered in that habitat (or most likely to be attracted to a trap). In 1988, C. excitans was dominant in the open habitats, with up to 75% of the catch in those habitats, but comprised much less of the catch in the woods (34%). Chrysops furcatus was a predominantly open habitat species but the distinction was not as marked. Both C. frigidus and C. zinzelus made up a greater percentage of the catch in the woods, 30% and 17% respectively, than in any of the open habitats.

In both 1989 comparisons, the difference in species

Figure 7. Percent of total tabanid catch in each habitat for four common Chrysops species in: A) woods, fen, bog, regrowth and road in 1988, B) fen, woods and regrowth in 1989 and C) bog, woods and road in 1989.



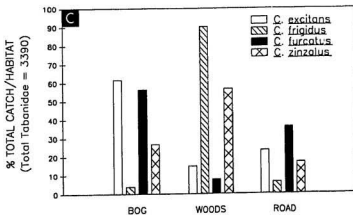
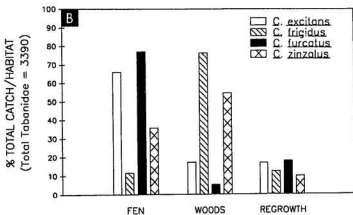
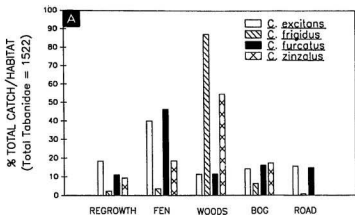
composition between the woods and open habitats was similar to the distribution observed in 1988. Chrysops excitans was again common in open habitats as was C. furcatus, although in the fen/woods/regrowth comparison, C. excitans was also proportionally high in the woods. As in 1988, C. frigidus and C. zinzalus were more common in the woods than in the open habitats making up, respectively, over 40% and 31% of the tabanids caught in the woods.

i) Chrysops excitans

An indication of species 'habitat preference' is given in the proportion of C. excitans trapped in a given habitat compared to its catch over all the habitats. The greatest percentage of this species was caught in the fen, during 1988 and in the first comparison from 1989 (Fig. 8A,B). It was trapped much less frequently in the woods and regrowth, in 1989, although its presence in those two habitats was roughly equal. Chrysops excitans predominated in the bog, in the bog/woods/road comparison of 1989, and was proportionally higher on the road than in the woods (Fig. 8C).

A Kruskal-Wallis test comparing numbers for this species in the different habitats supported the above trend of C. excitans as a species preferring open habitats, particularly open peatlands. In 1988, C. excitans was ranked highest in three open habitats, fen, regrowth and road, which were

Figure 8. "Habitat preference" of four common Chrysops species as given by percent of each species trapped in a habitat compared to total catch of that species in all habitats for: A) woods, fen, bog, regrowth and road in 1988, B) fen, woods and regrowth in 1989 and C) bog, woods and road in 1989.



significantly different from the woods and bog ($p < 0.05$). On a daily basis, the same trend was repeated for July 14 and July 16 of the same year, while the other four trapping days showed no significant differences between the five habitats. In the fen/woods/regrowth comparison of 1989, this species ranked significantly higher in the fen, as opposed to the woods and regrowth. Considering the days separately, June 28 and June 30 showed the same trend. The catch of C. excitans was significantly higher in the bog than in the woods or road during the second comparison of 1989 ($p < 0.01$); as it was, when days were considered separately, on July 21.

ii) Chrysops frigidus

Catches of C. frigidus were always ranked highest in the woods in all comparisons of abundance between habitats (Fig. 8). Results of the Kruskal-Wallis test and Tukey-type comparison confirm that C. frigidus was trapped less frequently in open as compared to wooded areas. In 1988, the Tukey-type comparison indicated that, overall, the woods were significantly different from the other four habitats for this species ($p < 0.05$). On July 18, this species was trapped only in the woods, and the woods were ranked highest on the other days included in the comparison.

Overall, in the fen/woods/regrowth comparison of 1989, C. frigidus was ranked highest in the wooded area, which was

significantly different from the fen and regrowth. Considering days individually, the catch of this species in the regrowth was ranked lower than and significantly different from the other two habitats on three of the five days. In the bog/woods/road comparison of 1989, the bog was ranked lowest and was considered to be significantly different from the woods and road ($p < 0.05$); catches of this species were ranked highest in the woods on each day. On July 18 and July 24, the bog was ranked lowest and significantly different from the other two habitats, while on July 21, the road, not the bog, was ranked significantly lower.

iii) Chrysops furcatus

Chrysops furcatus was similar to C. excitans in its 'preference' for open habitats, particularly peatlands. It was trapped more commonly in the fen in 1988 (Fig. 8A) and the 1989 fen/woods/regrowth comparison (Fig. 8B), and most often in the bog during trapping in the 1989 bog/woods/road comparison (Fig. 8C). The differences between habitats in 1988 were not significant although the fen was ranked highest in all cases. In catches from the 1989 fen/woods/regrowth comparison, the fen and regrowth were ranked higher than and significantly different from the woods for C. furcatus ($p < 0.05$). The fen was ranked higher than the woods and regrowth on all days, on four out of five this difference was

included in the analysis on two of the six days in 1988 and on three of the nine days in 1989 due to low sample size. Although the difference between habitats was considered significant ($p < 0.05$) on July 14 and July 18, 1988, the Tukey-type test did not reveal where these differences were. On July 10 and 16, 1989, in the fen/woods/regrowth comparison, the woods were ranked higher and considered different from the regrowth. In the bog/woods/road comparison, the woods ranked highest and were significantly different ($p < 0.05$) from the road, on July 18, and from the bog on July 21.

4. Comparison of tabanid abundance within the same habitat type

A Kruskal-Wallis analysis did not reveal significant differences between the four Box trap sites within any of the habitats sampled during comparison of different habitats in 1989. Of the four traps in the woods, catches from the two traps in or on the edge of a clearing were almost always higher than catches from the two traps in the canopied forest, but the Kruskal-Wallis test did not indicate that these differences were significant.

For the 1988 comparison between three different wooded areas, a Kruskal-Wallis or Mann-Whitney comparison indicated that, although tabanid abundance in the dry woods was ranked highest on both trapping days, there was no significant

significant. For the second 1989 comparison between the bog, woods and road, the woods were ranked lowest, overall, and were significantly different from the bog and road ($p < 0.05$). In the first two days of this comparison, the bog was ranked significantly higher for C. furcatus than were the woods. The last two days were not significantly different but, again, the bog was ranked highest.

iv) Chrysops zinzelus

Chrysops zinzelus appeared to 'prefer' wooded areas (Fig. 8) although not to the same degree as C. frigidus. A greater percentage of C. zinzelus was trapped in the open peatlands (fen and bog) as opposed to the disturbed open areas (road and regrowth).

Like C. frigidus, this species was always ranked highest in the woods in terms of abundance, although such a ranking was not always significant. Its abundance in the woods in 1988 was considered significantly different from that in the fen, regrowth and road but not the bog ($p < 0.05$). In 1989, there was no significant difference in the abundance of this species between the fen, woods and regrowth but, in the bog/woods/road comparison of 1989, it was ranked lowest and significantly different on the road as compared to the bog and woods ($p < 0.05$).

Considering individual days, this species was not

difference ($p > 0.05$) in trap catches when compared to catches in a more canopied site and a site used as a bedding area by caribou. A comparison in 1989, using Manitoba traps in three different wooded areas and three different fens, again showed no significant differences in numbers of tabanids trapped. Catches of tabanids in three different regrowth areas were too low for analysis.

5. Direct comparison of Manitoba and Box traps

On July 18, 1988, two Box traps were operated in the fen and two in the bog where trapping was being carried out using Manitoba traps (also two traps/habitat). The Manitoba and Box trap catches were the most similar to each other for C. excitans, in both the bog and fen habitats (Table 4). The Manitoba traps caught 30 C. excitans in the bog, while 27 were trapped in the Box traps; in the fen, 69 C. excitans were caught in the Manitoba traps as compared to 73 in the Box traps. For all other species of Chrysops, higher numbers were caught in the Box traps (Table 4). The difference between traps was particularly noticeable for C. furcatus, of which 217 specimens were caught in Box traps and 17 in Manitoba traps, and C. zinzalus, of which 118 were trapped in Box traps and 3 in Manitoba traps. Neither type of trap caught many Hybomitra, but Manitoba traps collected a representative of three species of horse flies as compared to

Table 4. Total numbers of each tabanid species trapped in Box and Manitoba traps in a bog and a fen, July 18, 1988, NW Gander, NF.

	<u>Manitoba</u>			<u>Box</u>		
	Bog	Fen	Total	Bog	Fen	Total
<u>C. ater</u>	0	0	0	0	1	1
<u>C. excitans</u>	30	69	99	27	73	100
<u>C. frigidus</u>	0	0	0	1	9	10
<u>C. furcatus</u>	4	13	17	46	171	217
<u>C. sordidus</u>	0	1	1	4	1	5
<u>C. zinzalus</u>	3	0	3	59	59	118
<u>H. affinis</u>	1	0	1	0	0	0
<u>H. frontalis</u>	1	0	1	0	0	0
<u>H. lurida</u>	0	1	1	0	1	1
Totals	39	84	123	137	315	452

only one horse fly species in the Box traps.

A great deal of similarity can be seen between these trapping results and the relative species abundance recorded for 1988 and 1989 (Table 1), bearing in mind that some species such as C. frigidus are not common in either the bog or fen. In the Manitoba traps from 1988, C. excitans is far more common than C. furcatus and C. zinzalus. In the Box traps from 1989, C. furcatus is more abundant than C. excitans and C. zinzalus.

6. Correlation of trap catch with wind, temperature and visibility

There was no correlation between the average daily trap catch and maximum daily temperature in either 1988 or 1989. There was a strong, negative correlation, however, with average daily catch and average wind velocity (correlation coefficients for 1988=-0.708 and for 1989=-0.795). Visibility in the woods, as estimated by percent of target visible, was not correlated with differences in trap catch between the four sites in the woods.

B: SIMULIIDAE

1. Species present

Of the blackflies identified to species from the sticky trap and sweep net samples, over 95% were Eusimulium

euradminiculum Davies. Relatively few specimens of Prosimulium mixtum or Simulium venustum/verecundum were collected in the fen, regrowth or woods.

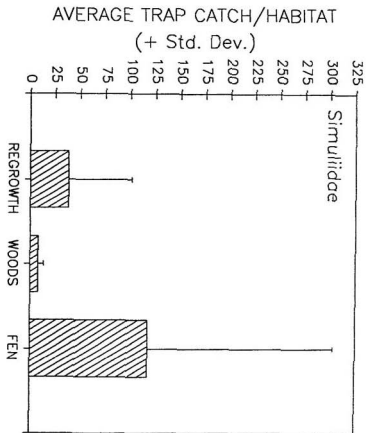
2. Comparison of blackfly abundance between different habitats

1) Sticky traps

Comparisons between habitats for total numbers of blackflies indicate primarily the distribution of Eusimulium euradminiculum, since this species was dominant in the collections. Collections from carbon-dioxide-baited sticky traps, operated for five days in a fen, wooded area and regrowth from June 15-21, revealed significant differences between habitats ($p < 0.01$). The fen and regrowth were significantly different from the woods, which was ranked lowest. The average trap catches in each habitat were 117.0 blackflies in the fen, 8.2 in the woods and 38.1 in the regrowth (Fig. 9).

On a daily basis, blackfly collections on four out of the five days showed significant differences between habitats, although the differences were not completely consistent. On all five days, the fen was ranked highest for blackfly abundance. On three days, catches in the fen were shown to be significantly different from those in the woods, but not from the regrowth. On one day, June 16, the catch of blackflies in the regrowth was ranked lowest and, on that day, different

Figure 9. Average trap catch of blackflies (+ one standard deviation) during comparison of abundance between fen, woods and regrowth using carbon-dioxide-baited sticky traps, June 15-21, 1989.



from catches in the fen.

ii) Landing counts

Landing counts with sweep net samples were carried out on four of the same days that the sticky traps were operating, June 15, 16, 20 and 21. A fen and a wooded area were sampled in both sweep net and sticky trap collections; the third habitat in sweep net sampling was a large clearing in the woods as opposed to a regrowth area as with the sticky traps. Although the three habitats sampled with the two collection methods did not correspond exactly, there were similarities in the collections if the regrowth and clearing are considered to be a similar habitat type.

For both methods of sampling on June 15, the wooded area was ranked lowest in terms of blackfly abundance and was considered significantly different from the fen and regrowth/clearing ($p < 0.05$). On June 16, however, the rank of abundance for the woods and regrowth/clearing was the opposite of the previous day, since abundance in the regrowth/clearing was ranked lowest and different from the other two habitats ($p < 0.05$).

The landing counts on June 20 only compared a fen and woods: the fen was always ranked higher than the woods and, in both the morning and afternoon, they were considered to be significantly different ($p < 0.05$). This was consistent with

the results of the June 20 bucket trapping which revealed catches in the fen to be higher than and significantly different from the woods. Landing counts were too low on June 21 to be included in the analysis.

3. Comparison of blackfly abundance within habitats

When the four trap sites within each habitat were compared to each other, there was no single trap which consistently had higher or lower trap catches.

DISCUSSION

A. TABANIDAE

1. Relative abundance of tabanid species

Collections at the NW Gander study site from 1988 and 1989 included all the species of Chrysops and all but two of the Hybomitra species, H. brennani (Stone) and H. longiglossa (Philip), which have been previously recorded for the island of Newfoundland (Philip 1962, Hudson 1977, Teskey 1990). Species from the two other genera recorded for the island, Tabanus and Atylotus (Teskey 1990), were not identified in the collections from the NW Gander site. Since A. thoracicus has never been observed to blood-feed, it may not have been attracted to traps which imitate a host, such as those used in the NW Gander study.

There are few studies for the province with which to compare the relative abundance of tabanid species as collected in the NW Gander area. Chrysops excitans, C. frigidus and C. furcatus, three of the four most commonly trapped species at the NW Gander site, were also the three most common species recorded at St. John's by McCreddie et al. (1985). The most common horse fly at the NW Gander site in 1988 was H. zonalis, as it was in the McCreddie et al. (1985) study. However, in

1989, both H. affinis and H. arpadi made up a greater proportion of the NW Gander catch. In general, there may be a lower abundance of tabanids in the St. John's area as compared to the NW Gander. Although the trapping efforts and collection methods were different in each study, McCreadie et al. (1985) trapped only 106 tabanids in a cattle-baited trap over a three and a half month period whereas NW Gander collections contained 1522 and 3390 specimens in 1988 and 1989 respectively.

Collections of tabanids from western Labrador using unbaited Manitoba traps (McCreadie and Colbo 1985), contained a very high proportion (64%) of C. excitans, as did the Manitoba trap catches from the NW Gander in 1988. Unlike the NW Gander collections which were also high in C. furcatus, C. frigidus and C. zinzalus, the next most common species in Labrador were C. ater and C. sordidus. The most common horse fly in the Labrador study was H. aequetincta, a species not present in insular Newfoundland.

A high proportion of Chrysops spp. compared to Hybomitra spp., as trapped in the NW Gander study, was also found in two Labrador studies (Brown and Morrison 1955, McCreadie and Colbo 1985) and in St. John's (McCreadie et al. 1985). However, catches from a study in New Brunswick (Lewis and Bennett 1977) contained proportionally more Hybomitra spp. (60.3%) than Chrysops spp..

i) Comparison of trap efficiency

Comparisons between studies in different locations reflect not only widespread differences in distribution of tabanids, but also differences in trap efficiency in collecting the various species present. Differences in the collections from Manitoba traps in 1988 and Box traps in 1989 at the NW Gander site, as well as the results from July 18, 1988 which directly compare these two trapping methods, indicate that different methods of sampling have an effect on the results obtained. Other studies which have used two or more sampling methods have also revealed differences in the proportions of species collected in different traps (Smith et al. 1970, Thibault and Harper 1983, Maire 1984). Roberts (1976) further illustrated trap differences in a direct comparison of six different tabanid traps. Besides general trap design, factors such as colour of trap and target, shape and height of target or amount of carbon dioxide may influence the collections in each trap.

The colour of the targets for both types of trap used in the NW Gander study was dark blue, and the traps were made from the same white netting, so the actual hue of the target or trap should not have been responsible for differences in attraction. Perhaps the Manitoba trap target, used in 1988, of a dark circle against the white background of the baffle presented a less obvious target than the contrast provided

simply by the canopy part of the trap. Contrast of the trap against the background is an important factor in attraction of tabanids (Roberts 1970, Allan and Stoffolano 1986) and, as Granger (1970) discovered, tabanids were attracted to the superstructure of a trap even when no target was present. Tabanids may have been attracted to the canopy or to the dark coloured collecting head of the NW Gander Manitoba trap. If they were not attracted specifically toward the target, as intended in the design of the trap, they would not enter the collecting jar. Manitoba traps would thus catch fewer tabanids than Box traps, since the Box traps had a much smaller area of white netting and no other dark focus points associated with the trap. Thomson and Saunder (1986) noted a reduced efficiency of Manitoba traps, compared to adhesive traps, and attributed it to the white appearance of the plastic canopy.

Although the type of target used in a trap has been reported to affect the tabanid catch (Matthysse et al. 1974), it would seem that target differences between the two NW Gander traps were not solely responsible for the differences in relative tabanid abundance. In 1989, the baffle target on the Manitoba traps was changed for a cluster of buckets but the pattern of species abundance remained relatively consistent. Similarly, Thomson and Saunder (1986) compared Manitoba traps which used either a standard black ball or

black adhesive panels as a target and found there was no difference in the trap catches caused by different targets.

Mullens and Gerhardt (1979) suggested that traps, such as the Manitoba canopy trap, which must be entered from the bottom probably select against species of tabanids which normally feed high up on the animal. At one NW Gander sampling site, several Chrysops spp. were observed flying around the Manitoba trap near the small piece of black pipe at the top (1.5 m high) rather than being attracted to the target nearer the ground. This observation is consistent with observations of feeding deer flies which often focus their feeding on the head, neck and antlers of caribou, deer and moose (M.H. Colbo pers. com., Smith et al. 1970) or on the highest point of an animal (Catts and Olkowski 1972). Although the flies observed around the top of the Manitoba traps at the NW Gander site were not identified to species, it is possible that greater attraction of certain species to the top rather than the bottom of the trap could have been partly responsible for the differences in relative abundance, as well as total catch, between the Box and Manitoba traps.

Height of the target was probably not a major factor contributing to trap differences in the NW Gander study, since the height of the targets in the two traps was similar. There seems to be a complex interaction between trap design and trap height which influences the relative abundance. Bennet and

Smith (1968) trapped more Tabaninae than Chrysopinae in Manitoba traps but, in the same area, trapped more Chrysopinae during an experiment using cylinder traps. They collected more tabanids on cylinders 12 inches (30.5 cm) rather than 36 inches (91.4 cm) from the ground, indicating that Chrysops, which predominated in their collections, were not necessarily higher fliers than Hybomitra.

The amount of carbon dioxide released as bait may also have an effect on the number and proportion of tabanids trapped (Roberts 1971, 1975). Trap catches in the NW Gander study could probably have been increased for both types of trap by increasing the amount of carbon dioxide used as bait. The calculated amount released in the present study (250 mL/min.) was less than the optimum of 1000 mL/min. suggested by Roberts (1971). Roberts (1971) also concluded that each tabanid species responds optimally to a particular release rate of carbon dioxide; thus the rate of carbon dioxide release could affect the relative abundance of species caught in the traps. This would not be a factor in explaining differences between the Box and Manitoba traps but may have influenced, to some extent, the proportion of species trapped as compared to that in other studies. Since Hybomitra spp. seem to prefer larger hosts than Chrysops spp. (Smith et al. 1970), increasing the amount of carbon dioxide released at the trap (as would be expected from a larger host (Roberts 1971))

might increase the proportion of Hybomitra spp. in collections from the NW Gander area.

Despite the wide range of factors which discourage a direct comparison of collections obtained from different sampling methods, it is possible to compare the results from studies in different locations which used the same sampling technique. The idea of a certain trap type being consistently attractive to certain species is supported by catches of tabanids in Box traps at the NW Gander site during 2 different years, 1989 and 1987 (Graham unpub.), which showed similar proportions of species trapped. As well, sweep net samples around a human collector in Algonquin Park, Ontario by both Smith et al. (1970) and Davies (1959) contained very similar relative abundances of tabanids. Manitoba traps, according to the results of several studies using such traps (Bennett and Smith 1968, Pechuman and Burton 1969, Thompson 1970, Matthyse et al. 1974, Golini and Wright 1978), are generally selective for Hybomitra as opposed to Chrysops. Comparing those results with collections from Manitoba traps in the NW Gander area, it appears that tabanid populations in the study area are comprised predominantly of Chrysops species rather than Hybomitra species.

The variability of results, depending on the collection method, suggests that the numbers and species of tabanids attracted to caribou or other hosts in the NW Gander habitats

differ from the proportion of tabanids collected in Manitoba and Box traps. Undoubtedly, the attractive features of any host are not exactly mimicked by a trap. However, a comparison of tabanid spatial distribution among habitats will reveal if there are inherent differences between habitats, and thus potential differences in degree of harassment experienced by a host, as long as the collecting technique is identical in each habitat.

2. Seasonal activity

i) Seasonal activity of tabanids

Flight activity of tabanids in Newfoundland has been recorded from late May to early September (Philip 1962). Maximum activity at the NW Gander site, as determined only through trapping for habitat comparisons rather than specific trapping to record seasonal activity, began in mid-June, peaked in July and started to decline by early August. This pattern of peak tabanid activity was similar to that found in New Brunswick (Lewis and Bennett 1977), Ontario (Davies 1959, Smith et al. 1970) and New Jersey (Thompson and Pechuman 1970) although the NW Gander season appeared to start slightly later and be of generally shorter duration.

The timing of peak tabanid activity and duration of activity will vary with differences in latitude, geographical location and the associated climatic conditions. In locations

with a more southerly latitude than the NW Gander area, tabanids tend to become active earlier in the season than in more northerly locations where they have a later, and shorter, season of seasonal activity. A study in southern Quebec (Thibault and Harper 1983) showed activity from early May to early August with a peak in June, while in northern Quebec, Maire (1984) recorded a shorter period of activity from mid-June to late-July with a peak in July. Baribeau and Maire (1983a) found a similar difference in tabanid activity between a temperate and a subarctic location. In Churchill, Manitoba, the seasonal activity was concentrated from the middle of July through August with a peak in early August (Miller 1951), about a month later than in the NW Gander area in Newfoundland and more southerly studies.

It has been suggested that temperature is the governing factor behind seasonal distribution (Davies 1959, Maire 1984, Tashiro and Schwardt 1953). At the NW Gander site, higher temperatures early in the summer of 1989 could have caused tabanid activity to peak slightly earlier than in 1988. A comparison of temperatures from mid-June to the end of the month shows, on average, temperatures higher by about 4 °C in 1989 (22.5 °C compared to 18.5 °C) for this time period. Similarly, Tashiro and Schwardt (1953), who recorded the onset of tabanid activity to be 10 days earlier in the second year of their study, attributed the earlier emergence of tabanids

to the relatively higher temperatures that year during the late spring and early summer as compared to their first season of collecting.

ii) Seasonal activity of individual species

In terms of species seasonality, there were also some similarities noted between the NW Gander site and other locations. Although the season of tabanid activity reported in other studies may have occurred earlier or later than in the NW Gander and may have been of greater or lesser duration, some species, relative to the others, were consistently early or late-season species. Generally, the early-season species, in the NW Gander area and in other studies, were C. ater (Lewis and Bennett 1977, Pechuman and Burton 1969, Thibault and Harper 1983), H. lurida (Lewis and Bennett 1977, Maire 1984, Thibault and Harper 1983, Smith et al. 1970) and H. affinis (Lewis and Bennett 1977, Teskey 1960). The species appearing later in the season were H. frontalis (Teskey 1960) and H. minuscula (Thibault and Harper 1983). Chrysops ater, C. excitans and C. frigidus appeared early in the season and had a relatively long period of activity as they did in studies by McCreadie and Colbo (1985) and Thibault and Harper (1983). Davies (1959) noted a seasonal change in the Tabanus spp. of Algonquin Park, Ontario, from species predominantly brown in colour, early in the season, to grey-coloured species

later in the year. This trend was also observed to a degree in the NW Gander area, where the Hybomitra species which were predominantly brown in colour, H. affinis and H. arpadi, appeared earlier in the season and ended their activity earlier than H. frontalis and H. frontalis, species more grey in colour.

Some of the activity patterns in other studies differed from those observed at the NW Gander study site. For example, H. frontalis, a late-appearing species in the NW Gander study, appeared relatively earlier in New Brunswick but continued its activity until late in the season (Lewis and Bennett (1977). Maire (1984) trapped H. lurida on the eastern shore of Hudson Bay where it had a relatively longer period of activity than C. excitans, C. furcatus and H. frontalis; the reverse of the NW Gander situation. Smith et al. (1970) found that C. sordidus had a longer period of activity than in the NW Gander site.

iii) Influence of weather on seasonal activity

Within the general pattern of peak seasonal activity, there are daily variations which are likely caused, at least in part, by variable meteorological factors. Temperature and cloud cover have been identified as two of the most influential environmental factors affecting tabanid activity (Burnett and Hays 1974, Joyce and Hansens 1968, Schulze et al.

1975). The effect of the above two factors was not ascertained in the NW Gander study since trapping was carried out on sunny, warm days in order to gather large numbers of tabanids for analysis of abundance between habitats. However, on July 14, 1988, when it became cloudy soon after the dry ice was set out, the lowest catch of the year was recorded (Fig. 4A). The cloudy weather on that day was also combined with a slightly lower maximum temperature. The decreased catch on June 30, 1989 (Fig. 4B) may have been related, not only to strong winds, but to the partly cloudy conditions.

Wind velocity was the only meteorological factor measured in the NW Gander study that was significantly correlated with tabanid activity. The peak of activity in both years, July 16 in 1988 and July 10 in 1989 (Fig. 4), were associated with very light winds. A rise in tabanid activity on July 18, 1989, as compared to the previous trapping day, was associated with calm weather. A decrease in activity on June 30, 1989 was, in the same way, associated with a day of strong winds. Burnett and Hays (1974) mentioned wind velocity change per hour as an influencing factor but noted that it seemed to be less important than barometric pressure, temperature, evaporation or sky radiation. Schulze et al. (1975) did not include wind velocity among the environmental factors in their predictive model and two other studies reported that tabanid activity was not at all related to wind speed (Joyce and

Hansens 1968, Alverson and Noblet 1977).

3. Spatial distribution

Other studies comparing spatial distribution of tabanids have involved habitats not directly comparable to those in the present study so a resemblance to results from the NW Gander study can only be suggested.

1) General distribution between habitats

In both years at the NW Gander study site, tabanids were, on average, more abundant in the woods as compared to the regrowth or road, both drier and less vegetated habitats (Fig. 6). Similarly, a Japanese study of tabanid habitat preference (Inaoka 1975) found tabanids to be more abundant in a forest than in a pasture or on the border of a pasture and forest. In New Jersey, observations of tabanids feeding on hogs indicated that herds in wooded areas were more subject to attack than those in open fields (Weiner and Hansens 1975).

Tabanid abundance in wooded areas in the NW Gander study site compared with that in two open peatlands, namely a fen and bog (Fig. 6), produced somewhat anomalous results. The fen was ranked higher than the woods in both years, whereas the bog was significantly lower than the woods in 1988 and ranked higher but not significantly so in 1989. A study of four habitats in the Laurentians, Quebec (Thibault and Harper

1983), using two community indices of productivity, found that a closed forest was less productive for tabanids than a bog lake. This is comparable to differences in abundance between the fen and woods in the NW Gander study. The greater amount of moisture in the NW Gander fen and the bog lake in the Quebec study, compared to that of the wooded areas or NW Gander bog, seems to be a common feature associated with greater tabanid abundance.

The results of some studies did not indicate a strong habitat preference for tabanids as a group. Thornhill and Hays (1972) concluded from their release and recapture experiments that the tabanids were equally distributed throughout the research area. Smith et al. (1970) found that tabanids in Algonquin Park, Ontario were generally uniformly distributed with the exception of one sylvan site, which may have been more favourable due to the presence of captive animals. However, several studies, including the above study by Smith et al. (1970), have revealed some definite habitat preferences for a number of individual tabanid species.

At the NW Gander location, Chrysops excitans was more abundant in the fen than in a wooded habitat. The same trend was found in Labrador by McCreadie and Colbo (1985) who showed this species preferred a fen (92.4% of the catch) as opposed to a wooded site (1.3%) when trapped with unbaited Manitoba traps. Of four habitats in a Quebec study (Thibault and

Harper 1983), C. excitans was far more abundant in the three open habitats, particularly near a bog lake, than in the woods.

The only other common species present at the NW Gander site that has been extensively studied elsewhere in Canada is C. frigidus. Whereas C. frigidus at the NW Gander site was associated predominantly with wooded areas, Golini and Wright (1978) noted a preference related to the degree of soil wetness. Perhaps the spatial distribution of this species is influenced by a combination of soil wetness and amount of forest canopy, since the habitats in which C. frigidus predominated in the Golini and Wright (1978) study appeared from the descriptions to be more densely wooded, as well as being generally wetter. Smith et al. (1970) described an anomalous distribution for C. frigidus since they trapped a greater proportion of this species along a river than in either of the wooded habitats, but collected it only rarely from a lakeshore.

A change in species composition may be effected through human alteration of habitat. The disturbance of forested areas by clear cutting, at the NW Gander study area, to form early successional stages (roads and regrowth) shifted the predominant species in the Chrysops community from C. frigidus and C. zinzalus to C. excitans and C. furcatus. In a similar manner, the species composition in an area of Japan (Inaoka

1975) experienced a shift in connection with advancing ruralization. Inaoka suggested that the clearing of forested land for agriculture brought about the observed changes in the tabanid assemblage in Hokkaido from a forest-eurytopic species complex predominating in Haematopota tristis Bigot to an openland-eurytopic complex with a predominance of Tabanus nipponicus Murdoch et Takahasi.

ii) Reasons for spatial distribution

Many factors, some of which are likely to interact, may explain the distribution of tabanids, on both the generic and species level, between different habitats. These factors include the relationship between larval and adult habitats, the ability of adults to disperse from the larval habitat, the presence of nectar sources in a habitat and the relative importance of vision and olfaction in host-seeking for different species. Daily variation in the general distribution patterns of tabanids between habitats may be caused by differences in the peak activity of species with different habitat preferences, variable weather conditions between days or the presence of host animals near the traps or in the study area. Some of the above factors, as well as differences in how traps are perceived by tabanids in different habitats, may cause or give the impression of a microhabitat preference.

a. Relationship between larval and adult habitat preference

The preferred larval habitat of a species may influence the likelihood of finding an adult in any particular habitat. A study in Japan indicated that the spatial distribution of adult tabanids was not directly related to the presence of potential hosts in a habitat but rather depended on the existence of larval habitats in the sampling sites (Hayakawa et al. 1989).

The larval habitats of some of the species found in the NW Gander area have been described briefly (Pechuman 1981, Teskey 1969). Tabanid larvae generally develop in mud, organic matter or moss in a damp or wet area, often near a lake or stream (Pechuman 1981). The larvae of Chrysops spp. and Hybomitra spp. are described by Chvála et al. (1972) as "hydrophilous" since they develop in or around water. Tashiro and Schwardt (1953) determined in their study that larval populations, especially Chrysops spp., are higher in wetter soil. Moss has been reported as a common substrate for larvae of C. excitans and C. frigidus and sphagnum moss, in particular, for H. lurida, H. frontalis, H. affinis and H. zonalis (Pechuman 1981, Baribeau and Maire 1983b). The larvae of C. ater have been reported to develop in slow-flowing streams (Teskey 1969) and in organic matter near the water's edge (Pechuman 1981).

Considering that damp moss and sphagnum are generally the larval habitats for many species trapped at the NW Gander site, the higher adult abundances in the fen, woods and bog, in 1989, and the lower abundance in the two drier, less mossy habitats (regrowth and road) support the study by Hayakawa et al. (1989) relating adult and larval habitats. As well, tabanid abundance was consistently high in the fen, which was the wettest of the five habitats and probably a highly favourable habitat for developing larvae. In 1988, though, the bog, a damp and mossy habitat, was often ranked among the habitats with the lowest abundance of tabanids indicating that factors, other than presence or close proximity of larval habitats, were affecting the trap catches.

Studies which address the distribution of C. frigidus, a species almost exclusively sylvan in the NW Gander study, do not support the idea that larval distribution is the governing factor behind adult distribution of this species. Baribeau and Maire (1983b) noted that larvae of C. frigidus were found in the open and not just the forested sections of a Quebec bog. Golini and Wright (1978) suggested that increased soil moisture favoured greater numbers of C. frigidus and, in a different study by James (1963), larvae of this species were found under leaf debris at the sloping edge of a pool. However, catches of this species in the fen at the NW Gander study site were much lower than in the nearby woods, a

tabanid adults and larvae in a bog and a fen in southern Quebec, found eight species of Hybomitra larvae of the thirteen adult species trapped but, of the twenty-one Chrysops species trapped as adults, larvae from only two species were collected. In their study, there was an obvious habitat preference by the adults of C. aestuans that did not seem to be related to the larval habitat; hundreds of adults were trapped in the fen and only two in the bog, but no larvae were collected from either habitat. Thus it would seem that, although there is some relationship between larval and adult habitats, factors other than larval habitat are also involved in the adult distribution.

b. Dispersal ability

The spatial distribution of adult females may be affected by their ability to disperse from the site where the larvae and pupae develop to a habitat where a potential host may be encountered. It is probable that tabanids could travel to all habitats within the 3.0 x 3.5 km² trapping area in the NW Gander study. In release and recapture experiments, Sheppard and Wilson (1976) trapped adults that had flown up to 6.8 km from the release point. As well, the inefficiency of localized insecticide control programs (Brown and Morrison 1955) could be explained by the ability of tabanids to make

comparatively drier habitat.

The adults of C. ater were trapped in all five habitats, often in traps which were not close to a slow-flowing stream or standing water, habitats where the larvae have been reported to develop. This species must either disperse quite a distance from the larval habitat or the possible larval habitats are more diverse than the ones listed above.

In some cases, there does seem to be a relationship between larval habitat and adult habitat preference. Teskey (1969) found larvae of H. miniscula predominantly in open areas. This corresponds well to the adult distribution in the NW Gander, where this species was trapped exclusively in open areas in 1988 and 70% in the open during 1989.

Several studies have specifically compared the larval habitat with that of the adult to determine if there was a relationship between the two. A study carried out in Hokkaido, Japan, revealed that larval habitats did not correspond exactly with those of the adult females but there appeared to be some relationship between the larval and adult habitats (Inaoka 1975). Of the tabanid species which had larvae found in the forest, two species were sylvatic as adults and two were eurytropic. Most, but not all, of the aquatic larvae were eurytropic as adults, and both species with larvae found in grasslands were preferentially openland species as adults. Baribeau and Maire (1983b), who sampled

long flights. Not all studies on tabanid dispersal have recorded long-distance flights. Bennett and Smith (1968) found that Tabaninae would travel up to 1 mile (1.6 km) away; Chrysopinae up to 1 1/4 miles (2.0 km), although they did not set traps at distances farther away. Thornhill and Hays (1972) placed traps up to a mile from the release point but found most of the recaptures within half a mile (0.8 km). However, even if most tabanids were restricted to approximately 1 km flights, members of the same population of tabanids would still be easily able to access, for example, the three habitats in the 1989 fen/woods/regrowth comparison all situated within an area of 1 km². The significant differences in abundance detected between these habitats indicates a species habitat preference rather than proximity to a breeding habitat.

c. Nectar feeding

Magnarelli et al. (1979), in a study of salt marsh tabanids in Connecticut, observed C. fuliginosus and C. atlanticus feeding on yarrow and swamp rose which grew on or near the salt flats where the adults of these species were active. The presence of various nectar sugars, often together with pollen grains, in over 90% of the deer flies tested, suggested to these authors an important association between

salt marsh tabanids and plants on which they feed. Studies on nectar feeding by tabanids were not carried out in the NW Gander study, but it is possible that the spatial distribution may have been affected to a degree by the presence of important nectar sources in various habitats.

Neither the study by Magnarelli et al. (1979), nor other investigations into nectar feeding (Kniepert 1980, Lewis and Leprince 1981), have proven whether tabanids can utilize a wide number of plant species within a habitat or whether they must seek out certain plants. However, a study by Wilson and Lieux (1972), which found up to 27 different pollen types in the guts of tabanids they collected, indicated that tabanids seek carbohydrates from a variety of plant sources. These authors also suggested that greater utilization of some plant species was due to the greater availability of those plants rather than a preference by the tabanids.

Habitats with no or limited vegetation, such as the road or early regrowth areas in the NW Gander study area, offer a paucity of nectar sources for tabanids. However, as discussed previously, the ability of tabanids to travel between habitats makes it unlikely that lack of nectar sources was an important factor in the decreased abundance of tabanids in the regrowth and road traps in the NW Gander study.

Although the presence of nectar sources may not play much of a role in the initial attraction of a tabanid to a host or

trap in a habitat, the lack of nectar sources may have an effect on the degree of harassment experienced by caribou, or other hosts, over a period of time in a habitat. Hughes et al. (1981) suggested that if the comfort movements of horses, which are standing on bare ground, prevent tabanids from landing and blood-feeding, eventually the flies will have to leave the animals in order to replenish energy reserves from carbohydrate sources on nearby vegetation. Thus, it would be advantageous for horses, or caribou, to move to an area of bare ground when tabanid activity is high. During the NW Gander study, there were many occasions during the afternoons of peak tabanid activity when caribou were observed standing or lying on bare roadways (pers. obs.)

d. Relative importance of olfaction and vision in
different habitats

A pattern of tabanid spatial distribution, as determined by trap catches in various habitats, may be influenced by whether the attractive features of a trap are visual, olfactory or a combination of both. Features of various habitats may affect the ability of tabanids to visually locate a host or trap, or to detect a source of carbon dioxide.

McCreadie and Colbo (1985) suggested that the visual attractiveness of a Manitoba trap (not baited with carbon dioxide) made this trap more efficient in an open fen as

compared to the woods, thus accounting for the extremely high proportion of Chrysops excitans they trapped in the fen. Smith et al. (1970), using only carbon dioxide as an attractant, reported C. excitans to be fairly ubiquitous throughout the four habitats they studied, implying that this species could detect carbon dioxide equally well in open and forested areas. The present study, which found C. excitans to favour open habitats, especially the fen, used a combination of visual and olfactory stimuli; the improved visibility of the target in the open habitats perhaps enhancing the efficiency of the traps in those habitats. On the other hand, Roberts (1977) found that carbon dioxide together with the presence of a black target did not significantly increase numbers of tabanids in a Malaise trap over those collected with carbon dioxide alone; thus he assumed the two attractants were sampling the same population.

The effectiveness of carbon dioxide bait may vary with habitat in a similar way that the efficiency of a visual attractant may be influenced by the habitat in which the host or trap is located. Helle and Aspi (1984) discovered that blood-sucking insects were trapped less frequently on a sandy riverbank than on a grassy meadow. They suggested that higher temperatures on the sand bank caused the air to warm up and rise, carrying carbon dioxide from the trap with it, and thus decreased the insects efficiency in locating the trap. This

theory would apply to the 1989 trapping results from the NW Gander study where the regrowth, which had patches of bare ground, and the road showed lower trap catches. Helle and Aspi (1984) suggested that the effect of bare ground on carbon dioxide dispersal explains the frequent use of sandy patches as resting places by reindeer and caribou during the insect season. As mentioned, caribou in the NW Gander area were also observed lying on dirt roads or bare, sandy patches during peak tabanid activity (pers. obs.). McElligott and McIver (1987) suggest that wind across open spaces is likely to disrupt the plumes of carbon dioxide. Since much higher numbers of tabanids were caught in the fen as compared to in the woods, in 1989, the visual attractiveness of the trap may have compensated for any disturbance of the carbon dioxide plumes.

McElligott and McIver (1987) suggest that the importance of visual cues and carbon dioxide depends on the habitat in which the tabanid is host-seeking; vision being of more importance in open areas and carbon dioxide alerting tabanids to the presence of a host in a wooded area where locating it visually would be difficult. The ability to utilize both senses effectively, depending on the habitat, is, they suggest, advantageous for tabanids. Thornhill and Hays (1972), who carried out mark and recapture experiments with tabanids in Alabama, mention that the amount of wooded terrain

in the flight path from the release point to the trap seemed to have no effect on the number of recaptures. They were using sticky cylindrical traps baited with carbon dioxide, a combination of visual and olfactory attractants which appeared to allow the tabanids to host-seek effectively no matter what the habitat.

It is possible that different species rely to varying degrees on olfaction and vision to locate their hosts. Chrysops frigidus, which was a primarily sylvan species in the NW Gander study, may be more efficient at locating a host using odour, as may C. zinzalus to a lesser degree. Chrysops excitans and C. furcatus, less than 20% of which were trapped in the woods, may rely more heavily on vision. It was observed, during the fen/woods/regrowth comparison of 1989, that before the ice was set out on some afternoons, some tabanids were already caught in the Box traps. They were absent from the two traps in the canopied woods but present in the traps in the clearings, fen and regrowth. This suggests that the target was an effective visual target in the open but ineffective, or effective only at close range after initial attraction to carbon dioxide, in the shaded woods. Bennett and Smith (1968) also concluded that sylvatic tabanids depend on stimuli in addition to vision in their host seeking since their cage traps, set in forested areas, were unsuccessful in capturing tabanids without the use of carbon dioxide.

e. Effect of individual species activity and habitat preference

In 1988, the two days which show statistical differences between habitats for tabanids as a group, July 14 and 16, are also the only two days where there were significant differences in the abundance of C. excitans between habitats. Considering the predominance of C. excitans in the 1988 collections, spatial distribution of this species influences the results for tabanids as a whole. C. frigidus demonstrated a preference for wooded areas throughout the season but, since it made up proportionately much less of the catch than C. excitans, it did not have the same impact on spatial distribution of tabanids as a group. C. frigidus did show a marked peak of activity on July 18, which equalized the abundance ranking of tabanids in the woods, which had a high catch of C. frigidus, and the fen, where C. excitans was predominantly active. Thus, differences in tabanid abundance between habitats, on that day, were not statistically significant using a Kruskal-Wallis test.

In 1989, the collections were not dominated by any one species, as was the case with C. excitans in 1988, thus the activity of any one species did not have such a marked effect on the perception of tabanid activity in general. Even though, in the bog/woods/road comparison, there were significant differences in abundance between habitats for each

of the four most common species, the preference of C. excitans and C. furcatus for the bog habitat and of C. frigidus and C. zinzalus for wooded areas decreased the differences in abundance for tabanids as a group between habitats in this comparison.

f. Effect of weather conditions

When a combination of seasonality and unfavourable weather conditions reduced the daily catch to low levels, slight variations in actual numbers became magnified using the system of ranks associated with the Kruskal-Wallis test. Low catches on July 14, 1988 and on June 28 and 30, 1989 were associated with a significant difference between habitats on those days. Certainly, there is a complex interaction between seasonality, and various important meteorological factors, such as wind, cloud cover and temperature, which makes it difficult to attribute daily differences to any one factor.

A study of interactions between horseflies and horses in the Camargue, France revealed a negative effect of wind speed on the landing rate of the tabanids, an effect considered separate from, although related to, the negative effect of wind on number of flies present around the horses (Hughes et al. 1981). These authors observed the horses moving to an open, bare area when tabanids became very abundant and active and suggested, assuming that wind speed is greater over bare

ground than over vegetation, that the horses were moving to an area with higher expected wind velocities. Strong winds on June 30 and July 21, 1989 probably contributed to the low catches in the regrowth and road respectively, areas with little or no vegetation, and thus emphasized differences in tabanid abundance when compared to the other habitats in the comparison.

Windy conditions may have affected the collecting efficiency of traps more in some habitats than in others. For example, the canopy part of the Manitoba trap tended to flap in the wind and some flies on the side of the trap may have been blown out before moving upwards to the collecting jar. Since the bog used in 1988 was more open, and windier, than any of the other habitats in the comparison, decreased efficiency of the Manitoba trap in collecting the attracted tabanids could have contributed to the low tabanid catches on the bog in that year.

g. Microhabitat preference

Several authors have mentioned a specific "microhabitat" preference for tabanids (Bennett and Smith 1968, Golini and Wright 1978). The latter authors discovered a majority of tabanid species were stratified within the first 100 m from a wooded area; collections decreased as traps were placed farther from the woods and toward an open hilltop. They

attributed this spatial distribution to a tendency for most species to remain close to the breeding ground, in the damp woods, and suggested that only a few species would disperse farther from their breeding sites. Bennett and Smith (1968), collected more tabanids in a trap placed in a clearing on a road through the woods than in traps near a lake, by a river or at another site on the road. They had no explanation for this apparent microhabitat preference.

At the NW Gander site, differences between given traps within a habitat were not statistically significant, but there was often great variation in tabanid abundance at the different traps. In the woods, during 1989 comparisons, these differences appeared to have some consistency; the traps in the canopied woods generally caught less than those placed in clearings in the woods. The ground in the clearings was drier and there was less moss than in the canopied woods, thus it seems unlikely that distance from the preferred larval habitat, as Golini and Wright (1978) suggested, would have had a great effect on the "microhabitat" distribution of the adults. In the fen, the differences between trap catches was quite large on some days but there was no obvious pattern to which catches were high and which low. Variable meteorological factors, such as changing wind conditions or degree of cloudiness, may have influenced the ability of the flies to locate the trap but there was no statistical

correlation between individual trap catches and meteorological factors.

The interaction of a trap, or a particular feature of a trap, with the surrounding environment may influence the ability of tabanids to perceive the trap and thus, in some cases, could give the impression of a microhabitat preference. At the four different trap locations in the woods, vegetation concealed the target to different degrees, but there was no significant correlation with a visibility index, estimating the percent of the target which was visible, and the average trap catch at each site. Perhaps the amount of reflected light from the target, rather than the percent of the target visible, was a factor in the apparently lower trap catches from the two sites in the shaded woods. Since attractiveness increases with the number of surfaces reflecting sunlight along paths parallel to the ground (Thorsteinson et al. 1966), the two traps in or alongside a clearing, where sunlight could reflect off the bucket target, may have been more attractive than the two in the canopied woods where the target would presumably be less reflective. As Roberts (1970) found out when measuring reflected light from Malaise traps, the reflectance values will vary depending on the relationship of the trap side to the angle of incidence of sunlight. Thus the visibility of a trap in open habitats may not be equivalent in all directions and could play a role in creating highly

variable catches between traps in the open.

h. Presence of animals

Several studies have suggested that the presence of host animals near tabanid traps may increase the catch in those traps (Golini and Wright 1978, Matthyse et al. 1974, Smith et al. 1970). The presence of caribou near the traps in the NW Gander study was not monitored while the traps were operating but caribou were observed in the vicinity of the traps at other times. Since caribou were widely dispersed and move frequently within an area, it is not likely they remained near traps long enough to significantly affect the results.

4. Relationship of trap catches to number and species of tabanids biting caribou

Since the Box traps and Manitoba traps used in this study did not at all resemble woodland caribou, the attractive features of the trap were likely perceived differently by tabanids than an actual host would be perceived. Not only were visual features different, but the amount of carbon dioxide being emitted from the traps, which has a relationship with the response of individual species (Roberts 1971), was probably much less than that normally given off by a caribou. Therefore, the composition of the trap collections cannot be assumed to reflect the number and species of tabanids

harassing caribou in the study area.

A number of studies illustrate a difference between trap catches and the proportion of tabanids harassing animals or show a definite host preference that is not discriminated by the traps. Weiner and Hansens (1975) noticed that Tabanus atratus commonly fed on hogs in New Jersey but was rarely captured in traps set up near the animals. C. frigidus was collected in low numbers by Lewis and Bennett (1977) in New Brunswick, but it was the most abundant species of Chrysops attracted to and observed feeding on cattle in the area. The same species, although an infrequent pest of man in Algonquin Park, Ontario as determined in sweep net sampling (Smith et al. 1970), comprised 26% of the Chrysopinae collected from deer and 17% of those collected from moose. In contrast to the above studies, though, is a study by Roberts (1972), who discovered no significant difference in catches between Malaise traps baited with carbon dioxide or with a steer.

The various species of tabanids will have different host preferences or have a different effect on their hosts, making some species greater pests than others. The number of deer flies was generally lower than the number of horse flies feeding on hogs in a study by Weiner and Hansens (1975). These two authors also noted some differences in the tabanid species biting horses and hogs. The size of the blood meal that is taken will vary with species. Thomas and Gooding

(1976) found that H. affinis takes between 42.0 - 133.9 Mg of blood as compared to C. furcatus which takes 17.2-41.6 Mg.

The relative numbers of tabanids present in a habitat, as indicated by trap catches, may not be directly related to the number landing on and thus harassing caribou or other hosts. Hughes et al. (1981) noticed that horses in the Camargue, France would move to a bare area when tabanid activity increased but such a move apparently did not decrease the numbers of tabanids on or about the horses. Rather, the landing rate of flies was reduced perhaps due to wind effects, thus reducing the harassment level, and seemed to be partly independent of the number of tabanids in the air around the horses.

The apparent preference of certain tabanid species in the NW Gander study area for either a wooded or an open habitat, as demonstrated by their differing abilities to locate a trap in the different habitats, imply that there are real differences in tabanid abundance between habitats. However, all of the common species were trapped in each of the habitats sampled. This indicates that in an area where potential hosts move between open and forested habitats, the tabanids in those habitats are equipped to some degree to locate the hosts in whichever habitat they are situated.

The results of this study do not indicate that forested areas provide an "insect-relief" habitat for woodland caribou.

In fact, roads and regrowth areas created by clear-cut logging operations had fewer overall numbers of tabanids. Before more can be said about the effect of habitat alteration on the degree of tabanid harassment experienced by caribou in the area, more must be known about the host preferences of the tabanid species which were collected in the present study.

B. SIMULIDAE

1. Relative abundance of blackfly species

The species Eusimulium eurvadminiculum, which made up the majority of the blackflies caught in the present study, is known from other studies to be ornithophilic (Bennett and Fallis 1971). The other two species identified in the NW Gander study, Prosimulium mixtum and Simulium venustum/verecundum, are considered mammalophilic (Lewis and Bennett 1973, McCreadie 1983). It is unlikely that Eu. eurvadminiculum would contribute much to the harassment of caribou in the area except, perhaps, as a minor annoyance if these flies were initially attracted to carbon dioxide produced by the caribou. Eusimulium spp. comprised less than 1% of the collections by Martin (1987) near St. John's using the same type of trap and has not, in general, been widely collected in Newfoundland (Lewis and Bennett 1973, McCreadie 1983, Pickavance et al. 1970).

2. Spatial distribution

There was a noticeable preference of Eusimulium euryadminiculum for the fen habitat; relatively few were collected in the wooded areas. As Bennett and Fallis (1971) discovered, the distribution of Eusimulium euryadminiculum (reported as Simulium euryadminiculum Davies) was concentrated at or near the shorelines of lakes and rivers and suggested an adaptation to the preferred environment of their host, the common loon. The spatial distribution of this species in the NW Gander study may be related to that of their host, since the fen in the comparison lay along the Owl Pond system of streams and ponds and was a suitable habitat for loons and other large waterfowl. Although loons were never sighted, they were often heard calling in the area around the fen.

The results of the blackfly trapping support the idea that host-seeking flies do have habitat preferences or, at least, their ability to detect a host differs in different habitats. Trapping methods used in this study to compare relative abundance of tabanids and blackflies between habitats are able to elucidate some of these habitat preferences or differences in host detection in different habitats.

SUMMARY

1. A total of 4912 tabanids were collected at the NW Gander study site in central Newfoundland using modified Manitoba traps, from July 5-24, 1988, and Box traps, from June 28-July 24, 1989; all traps were baited with carbon dioxide. Eight species of Chrysops and seven species of Hybomitra were collected; Chrysops spp. made up over 93% of the catch in both years. Four species were consistently common: C. excitans, C. frigidus, C. furcatus and C. zinzelus.

2. Tabanid activity, as determined by trap collections consisting primarily of Chrysops species, peaked in mid-July in both years. The peak of activity several days earlier in July, 1989 may be attributed to warmer temperatures in June and early July of 1989 as compared to the 1988 season. C. ater, H. affinis and H. lurida generally appeared early in the season; H. minuscula and H. frontalis were late-season species.

3. In 1988, differences in tabanid abundance between five habitats: woods, fen, bog, regrowth and road were revealed using a non-parametric Kruskal-Wallis analysis. The fen was

generally ranked highest for tabanid abundance while abundance in the bog and road was often significantly lower than in the other habitats.

4. In 1989, a comparison between fen, woods and regrowth ranked the regrowth significantly lower than the other two habitats in terms of total tabanid abundance; the fen was always ranked highest on each day of trapping. In a comparison between bog, woods and road habitats, no significant difference was detected although catches from traps on the road were ranked lowest on each day.

5. Of the four most commonly trapped species, C. excitans showed a slight preference for open areas, C. furcatus was trapped predominantly in open habitats, C. frigidus and C. zinzalus appeared to be preferentially although not exclusively sylvan. It would appear that clearing of forested land in the NW Gander study area leads to a change in species composition from species which are trapped predominantly in wooded areas, C. frigidus and C. zinzalus, to preferentially open-land species, C. excitans and C. furcatus. Species of Hybomitra were trapped in numbers too low for analysis.

6. The Manitoba trap used in this study was slightly more efficient than the Box traps in collecting Hybomitra species

but was much less efficient for Chrysops species. The Manitoba trap collected predominantly C. excitans whereas the Box trap collected proportionally more C. furcatus, C. zinzalus and C. frigidus.

7. There was a strong negative correlation between average daily trap catch and average wind velocity. No correlation was apparent between catch and average temperature or catch and target visibility.

8. Although a variety of factors may influence spatial distribution among different habitats, including proximity to larval habitats, ability to disperse from the larval to adult habitat and presence of nectar sources, the present study did not attempt to elucidate the effect of such factors on tabanid distribution. However, more tabanids were collected from moist, mossy habitats (fen, woods, bog), which likely contained suitable larval habitats, than from the drier habitats (regrowth, road).

9. Collections with Manitoba and Box traps indicate that there are differences in abundance and species composition between habitats. However, this may not reflect differences in the degree of harassment experienced by woodland caribou in each of the habitats studied. It is not known if certain

tabanid species are greater pests of caribou than others, or whether differences in tabanid abundance between habitats are significant enough for caribou to select habitats with a lower abundance as a response to harassment. Since all the common tabanid species were trapped in each habitat, it appears they are equipped, to some degree, to locate hosts in both wooded and open habitats.

10. Over 95% of the blackfly collections consisted of Eusimulium euryadminiculum, a species which showed a marked preference for the fen habitat as opposed to a wooded area or regrowth. Distribution of this species may be related to the distribution of its hosts, usually waterfowl, along a series of lakes and wetlands which included the fen where trapping was carried out.

11. The results of the blackfly trapping support the idea that host-seeking flies do have habitats preferences or, at least, their ability to detect a host (trap) differs in different habitats.

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APPENDIX A

The date, habitats sampled and total number of tabanids collected during trapping at the NW Gander study area in 1988 and 1989.

Collections in 1988 were made using Manitoba traps (except for July 18). In 1989, comparisons between different types of habitats used Box traps; comparisons of the same type of habitat used Manitoba traps.

Date	Habitats	# Tabanidae
July 5, 1988	Regrowth, Fen, Woods, Bog, Road	189
July 8, 1988	Regrowth, Fen, Woods, Bog, Road	145
July 14, 1988	Regrowth, Fen, Woods, Bog, Road	63
July 16, 1988	Regrowth, Fen, Woods, Bog, Road	450
July 18, 1988	Regrowth, Fen, Woods, Bog, Road	299
July 24, 1988	Regrowth, Fen, Woods, Bog, Road	376
July 10, 1988	Three different wooded sites	608
July 18, 1988	Fen, Bog (Box traps)	452
June 28, 1989	Fen, Woods, Regrowth	90
June 30, 1989	Fen, Woods, Regrowth	102
July 3, 1989	Fen, Woods, Regrowth	481
July 10, 1989	Fen, Woods, Regrowth	1111
July 16, 1989	Fen, Woods, Regrowth	512
July 18, 1989	Bog, Woods, Road	554
July 19, 1989	Bog, Woods, Road	318
July 21, 1989	Bog, Woods, Road	124
July 24, 1989	Bog, Woods, Road	99
July 10, 1989	Three different wooded sites	217
July 13, 1989	Three different wooded sites	99
July 14, 1989	Three different wooded sites	107
July 16, 1989	Three different fens	126
July 17, 1989	Three different fens	93
July 18, 1989	Three different fens	206
July 24, 1989	Three different regrowth areas	25
July 26, 1989	Three different regrowth areas	12
Aug. 1, 1989	Three different regrowth areas	5

APPENDIX B

The date, habitats sampled and total number of blackflies collected during sampling at the NW Gander study area in 1989.

Date	Habitats	Collection Method	# Simuliidae
June 15	Fen, Woods, Regrowth	Sticky trap	2313
June 16	Fen, Woods, Regrowth	Sticky trap	211
June 18	Fen, Woods, Regrowth	Sticky trap	70
June 20	Fen, Woods, Regrowth	Sticky trap	342
June 21	Fen, Woods, Regrowth	Sticky trap	348
June 15	Fen, Woods, Clearing	Landing counts	395
June 16	Fen, Woods, Clearing	Landing counts	182
June 20	Fen, Woods	Landing counts	327

